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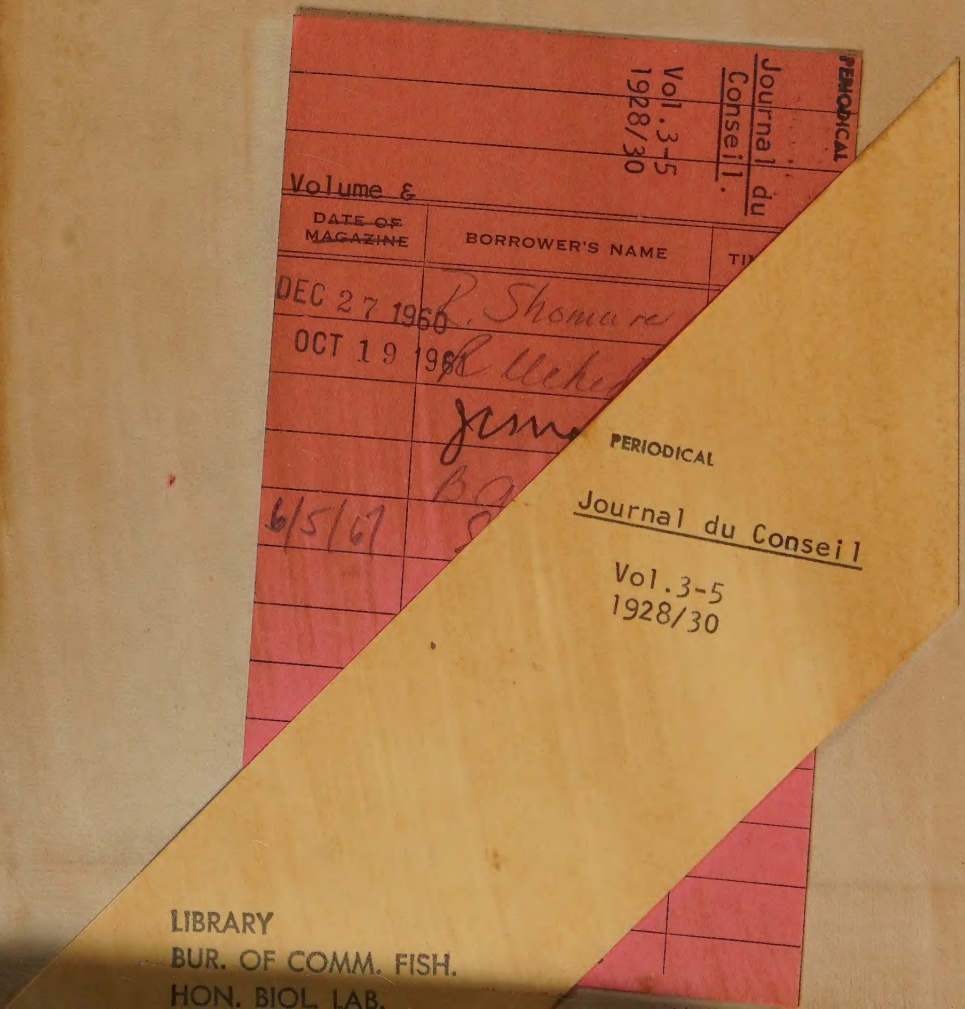

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POUR L'EXPLO[illegible]ON DE LA MER

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IMPRIMERIE BIANCO LUNO

Variations and Fluctuations of the Number of Individuals in Animal Species living together.

By

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Translated by Miss **Mary Evelyn Wells,** Doctor of Mathematics.

§ 1. Preliminary Considerations.

1. Many applications of mathematics have been made to biology. In the first place come the researches on physiological questions relative to the senses, to the circulation of the blood, to the movement of animals, which can be viewed as subjects of optics, of acoustics, of hydrodynamics or of the mechanics of solid bodies and hence have not called for new methods outside the scope of the classical mathematical physics. Biometry, on the other hand, with its own modes of procedure, has recourse to the use of calculus of probability and has created a mass of new and original studies[1]). And too the recent geometrical researches on the form and growth of organized existence have a particular character. In them geometry has been used to describe the forms themselves and their development just as for a long time it has been employed in astronomy to describe the orbits and the motions of the celestial bodies[2]). Moreover it is to be hoped that the methods allied to the analysis used for heredity may be advantageously employed in questions concerning biology[3]).

Putting aside other applications of mathematics, these points, of

[1]) Cf. Volterra, Saggi scientifici. — I. Sui tentativi di applicazione delle matematiche alle Scienze biologiche e sociali, Bologna, Zanichelli, 1920. — For Biometry see the periodical "Biometrika" founded by Karl Pearson in 1901.

[2]) D'Arcy Thompson Wentworth, On Growth and Form, Cambridge, 1917.

[3]) Volterra, Ibid., VII, L'evoluzione delle idee fondamentali del calcolo infinitesimale. — VIII, L'applicazione del calcolo ai fenomeni d'eredità.

which I shall speak in this article, I consider worthy of study and research, as being able to clarify various points actually interesting to biologists[1]).

2. Biological associations (biocoenosis) are established by many species which live in the same environment. Ordinarily the various individuals of such an association contest for the same food, or else some species live at the expense of others on which they feed. But nothing prevents them from being able to take advantage of each other. All this comes back again to the general phenomenon called the struggle for life.

The quantitative character of this phenomenon is manifested in the variations of the number of individuals which constitute the various species. In certain conditions such variations consist in fluctuations about a mean value, in others they show a continuous decrease or increase of the species.

The study of these variations and of these different tendencies is important theoretically, but often has also a practical importance worthy of notice, as in the case of the species of fish which live in the same seas and whose variations interest the fisheries[2]). And also agriculture is

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[1]) The complete work has been published by me in "Memorie della R. Accademia Nazionale dei Lincei", division on mathematical, physical and natural sciences, Series VI, vol. II, and in Memoria CXXXI, of R. Comitato Talassografico Italiano, with the title: Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. After the publication of this note I received word that in the study of parasites relative to malaria there existed the equations of Ross, and I learned that in the volume: Elements of physical Biology, New York 1925, Doctor Lotka had considered the case of two species developed by me in § 3 of part 1, arriving by other methods at the integral, to his diagram, and to the period of small oscillations. However the general laws obtained by me in this same section, the various cases developed in the other sections of the first part, as likewise all the other three parts of my Memoir, in which I consider the applications of the aforesaid laws and the cohabitation of n species in the hypothesis of conservative and dissipative associations, are new and treated for the first time.

[2]) Doctor Umberto D'Ancona has many times spoken to me about the statistics which he was making in fishery in the period during the war and in periods before and after, asking me if it were possible to give a mathematical explanation of the results which he was getting in the percentages of the various species in these different periods. This request has spurred me to formulate the problem and solve it, establishing the laws which are set forth in § 7. Both D'Ancona and I working independently were equally satisfied in comparing results which were revealed to us separately by calculus and by observation, as these results were in accord; showing for instance that man in fisheries, by disturbing the natural condition of proportion of two species, one of which feeds upon the other, causes diminution in the quantity of the species that eats the other, and an increase in the species fed upon. See: D'Ancona, Dell' influenza della stasi peschereccia del periodo 1914—18 sul patrimonio ittico dell' Alto Adriatico. Memoria CXXVI R. Comitato Talassografico Italiano.

interested in the fluctuations of parasites of plants when these parasites are attacked by parasites of these parasites. Also infective diseases (malaria etc.) show fluctuations which are probably of an analogous nature.

The question presents itself in a very complex way. Certainly there exist periodic circumstances relating to environment, as would be those, for example, which depend upon the changing of the seasons, which produce forced oscillations of an external character in the number of individuals of the various species.

These actions of external periodic nature were those which were specially studied from the statistical point of view, but are there others of internal character, having periods of their own which add their action to these external causes and would exist even if these were withdrawn?

Observation inclines to an affirmative reply and mathematical calculation confirms it, as we shall see in this article. But on first appearance it would seem as though on account of its extreme complexity the question might not lend itself to a mathematical treatment, and that on the contrary mathematical methods, being too delicate, might emphasize some peculiarities and obscure some essentials of the question. To guard against this danger we must start from hypotheses, even though they be rough and simple, and give some scheme for the phenomenon.

For that we shall begin by studying that which could be called the purely internal phenomenon, due only to the reproductive power and to the voracity of the species as if they were alone. Later we shall study the addition of foreign or forced periodic actions which are the result of environment.

3. And what mathematical methods will it be convenient to use? Perhaps the methods founded on the calculus of probability which might suggest themselves first? Let me say at once it is not these which lead us to the goal.

Permit me to indicate how the question can be considered: Let us seek to express in words the way the phenomenon proceeds roughly: afterwards let us translate these words into mathematical language. This leads to the formulation of differential equations. If then we allow ourselves to be guided by the methods of analysis we are led much farther than the language and ordinary reasoning would be able to carry us and can formulate precise mathematical laws. These do not contradict the results of observation. Rather the most important of these seems in perfect accord with the statistical results[1]). The road followed is thus

[1]) D'Ancona establishes from the examination of the statistics of the markets of Trieste, Venice and Fiume that during the war there took place in the Upper Adriatic

clearly indicated with these few words. We shall see after a little how the difficulties met were overcome.

4. On the basis of the ideas expressed above, in order to simplify the treatment, we shall assume that the species increase or decrease in a continuous way, that is to say we shall assume that the number which measures the quantity of individuals of a species is not an integer, but any real positive number whatever which varies continuously. In general the hatchings take place in definite periods separated from each other by an interval of time; we shall neglect these particulars assuming that births may take place with continuity every moment and that, on a parity with all the other conditions, they may be verified proportionally to the number of living individuals of the species. Let the same assumption be made on death and, according as births may prevail over deaths, or vice versa, an increase or diminution of individuals will occur. Thus we shall assume the homogeneity of the individuals of each species neglecting the variations of age and size.

If there is only one species or if the others have no influence on it, so that the circumstances of birth and death do not vary, we shall have, if N denotes the number of individuals,

$$\frac{dN}{dt} = nN - mN = (n-m)N$$

where t denotes time and n and m are constants, respectively the coefficients of birth and mortality. Letting $n - m = \varepsilon$ we shall have

$$\text{(I)} \quad \frac{dN}{dt} = \varepsilon N, \qquad \text{(II)} \quad N = N_0 e^{\varepsilon t}$$

where N_0 denotes the number of individuals at the time zero. ε will be called the coefficient of increase of the species and if it is positive there will be a true increase, otherwise a decrease. If the circumstances of birth and death change, ε will vary with time or with N or with other elements. In such a case (I) will always exist, but evidently we shall no longer have (II).

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a change of the proportions of the individuals of the various species of fish to the advantage of the Selacians which must be considered among the most voracious. This result agrees with the law of the disturbances of the average which we express farther along.

§ 2. Biological Association of two Species which contend for the same Food.

1. Let us suppose we have two species living in the same environment: let the numbers of the individuals be respectively N_1 and N_2 and let ε_1 and ε_2 be the values which their coefficients of increase would have if the quantity of the common food were always such as to amply satisfy their voracity. We shall have

$$\frac{dN_1}{dt} = \varepsilon_1 N_1, \quad \frac{dN_2}{dt} = \varepsilon_2 N_2 \qquad (\varepsilon_1 > 0, \quad \varepsilon_2 > 0).$$

Let it be admitted now that the individuals of the two species, continually increasing in number, diminish the quantity of food of which each individual can dispose. Let us suppose that the presence of the N_1 individuals of the first species diminishes this quantity by an amount $h_1 N_1$ and the presence of the N_2 individuals of the second species diminishes it by the amount $h_2 N_2$ and that therefore by the combination of the two, the diminution amounts to $h_1 N_1 + h_2 N_2$ and that by virtue of the unequal need of food of the two species, the two coefficients of increase are reduced to

[1] $$\varepsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2), \qquad \varepsilon_2 - \gamma_2 (h_1 N_1 + h_2 N_2)$$

We shall then have the differential equations

[2_1] $$\frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2)) N_1$$

[2_2] $$\frac{dN_2}{dt} = (\varepsilon_2 - \gamma_2 (h_1 N_1 + h_2 N_2)) N_2$$

in which we must suppose ε_1, ε_2, h_1, h_2, γ_1, γ_2 to be positive constants.

2. From the preceding equations it follows that

[3_1] $$\frac{d \log N_1}{dt} = \varepsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2)$$

[3_2] $$\frac{d \log N_2}{dt} = \varepsilon_2 - \gamma_2 (h_1 N_1 + h_2 N_2)$$

and hence

[4] $$\gamma_2 \frac{d \log N_1}{dt} - \gamma_1 \frac{d \log N_2}{dt} = \varepsilon_1\gamma_2 - \varepsilon_2\gamma_1$$

that is to say

[5] $$\frac{d \log \frac{N_1^{\gamma_2}}{N_2^{\gamma_1}}}{dt} = \varepsilon_1\gamma_2 - \varepsilon_2\gamma_1$$

and integrating and passing from logarithms to numbers,

[6] $$\frac{N_1^{\gamma_2}}{N_2^{\gamma_1}} = Ce^{(\varepsilon_1\gamma_2 - \varepsilon_2\gamma_1)t}$$

where C is a constant quantity.

3. If the binomial $\varepsilon_1\gamma_2 - \varepsilon_2\gamma_1$ is not zero we can suppose it positive, for if it were not positive it would suffice to exchange species 1 with species 2 to make it positive.

In this case

$$\lim_{t=\infty} \frac{N_1^{\gamma_2}}{N_2^{\gamma_1}} = \infty .$$

For N_1 equal to or greater than $\frac{\varepsilon_1}{\gamma_1 h_1}$, by virtue of $[2_1]$, the differential coefficient $\frac{dN_1}{dt}$ is negative, hence N_1 can not exceed a certain limit.

N_2 then must approach zero.

It is easy to compute the expression asymptotic to N_1.

In fact when N_2 becomes small enough to remain negligible, equation $[2_1]$ will become

$$\frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 h_1 N_1) N_1$$

or, separating the variables

$$dt = \frac{dN_1}{N_1(\varepsilon_1 - \gamma_1 h_1 N_1)}$$

and integrating and passing from logarithms to numbers,

$$\frac{N_1}{\varepsilon_1 - \gamma_1 h_1 N_1} = C_o e^{\varepsilon_1 t}$$

C_o being a constant. Hence

$$N_1 = \frac{C_o \varepsilon_1 e^{\varepsilon_1 t}}{1 + \gamma_1 h_1 C_o e^{\varepsilon_1 t}} = \frac{C_o \varepsilon_1}{e^{-\varepsilon_1 t} + \gamma_1 h_1 C_o}$$

Therefore N_1 approaches asymptotically the value $\frac{\varepsilon_1}{\gamma_1 h_1}$ for increasing or decreasing values according as C_o is positive or negative.

We can sum up the results we have obtained, in the following proposition: If $\frac{\varepsilon_1}{\gamma_1} > \frac{\varepsilon_2}{\gamma_2}$ the second species continually decreases and the number of individuals of the first species approaches $\frac{\varepsilon_1}{\gamma_1 h_1}$.

§ 3. Association of two Species one of which feeds upon the other.

1. Let N_1 and N_2 be the numbers of individuals of the two species. Let $\varepsilon_1 > 0$ represent the coefficient of increase which the first would have if the other did not exist. Let us suppose that the second would die out because of lack of food if it were alone; therefore let its coefficient of increase be negative and equal to $-\varepsilon_2$ (ε_2 can be considered as a coefficient of decrease). If each of the two species were alone we should have

$$[7_1] \quad \frac{dN_1}{dt} = \varepsilon_1 N_1, \qquad [7_2] \quad \frac{dN_2}{dt} = -\varepsilon_2 N_2.$$

But if they are together and the second species feeds upon the first ε_1 will diminish and $-\varepsilon_2$ will increase, and evidently the more numerous the individuals of the second species become the more ε_1 will diminish, and the more the individuals of the first species increase, the more will $-\varepsilon_2$ increase. To represent this fact in the simplest manner let us suppose that ε_1 diminishes proportionally to N_2, that is by the amount $\gamma_1 N_2$, and that $-\varepsilon_2$ increases proportionally to N_1, that is by the amount $\gamma_2 N_1$.

We shall have then the differential equations

$$(A_1) \quad \frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2) N_1, \qquad (A_2) \quad \frac{dN_2}{dt} = (-\varepsilon_2 + \gamma_2 N_1) N_2.$$

The assumption that the coefficients of increase and of decrease be respectively linear in relation to N_2 and N_1 may seem very loose, but

it is justified as we shall see in § 5, if we compute these coefficients by means of the probable number of encounters of the individuals of the two species. And even if we take for the coefficients any functions whatever of N_2 and N_1 respectively, the mode of integration used in this section, in which they are supposed linear, works out just the same.

2. While the constants ε_1 and ε_2 sum up the conditions of birth and death of the two species, the coefficients γ_1 and γ_2 measure in a numerical way the aptitude of the first species to defend itself and the means of offense of the second species. In fact if we increase these means of offense then γ_1 and γ_2 must increase, and if we increase the means of protection of the first species then a diminution of these coefficients must follow.

In order to have a method of measuring ε_1 and ε_2 it will be sufficient to integrate $[7_1]$ and $[7_2]$; we should have if each of these two species were alone

$$N_1 = C_1 e^{\varepsilon_1 t}, \qquad N_2 = C_2 e^{-\varepsilon_2 t},$$

where C_1 and C_2 are respectively the values of N_1 and N_2 for $t = 0$. Let us place $N_1 = 2C_1$, $N_2 = \frac{1}{2}C_2$ and denote by t_1 and t_2 the times necessary respectively for the first species to double itself and the second to be reduced by half. We shall have

$$\varepsilon_1 = \frac{\log_e 2}{t_1} = \frac{0.693}{t_1}, \qquad \varepsilon_2 = \frac{\log_e 2}{t_2} = \frac{0.693}{t_2}.$$

From this it follows that ε_1 and ε_2 have the dimensions -1 with respect to time. It would always be possible to take the units of time in such a way that $\varepsilon_1 = 1$. In fact if we take as the unit of time the time necessary for the first species to increase in the ratio $e = 2.728$, we shall have $e = e^{\varepsilon_1}$ and hence $\varepsilon_1 = 1$. ε_2 could be treated similarly.

Letting

[8] $$\frac{\varepsilon_2}{\gamma_2} = K_1, \qquad \frac{\varepsilon_1}{\gamma_1} = K_2,$$

the equations (A_1) and (A_2) show us that if

$$N_1 = K_1 \qquad N_2 = K_2 \qquad \text{then} \quad \frac{dN_1}{dt} = \frac{dN_2}{dt} = 0,$$

that is to say the two species are in a stationary state.

We shall have then

$$\gamma_1 = \frac{\varepsilon_1}{K_2}, \qquad \gamma_2 = \frac{\varepsilon_2}{K_1}.$$

Now let us pass to the integration of equations (A_1) and (A_2).

From (A_1) and (A_2) it follows that

$$[9] \qquad \frac{d\frac{N_1}{K_1}}{dt} = \varepsilon_1\left(1-\frac{N_2}{K_2}\right)\frac{N_1}{K_1}, \qquad \frac{d\frac{N_2}{K_2}}{dt} = -\varepsilon_2\left(1-\frac{N_1}{K_1}\right)\frac{N_2}{K_2},$$

whence, by placing

$$[10] \qquad N_1 = K_1 n_1, \qquad N_2 = K_2 n_2,$$

the preceding equations may be written

$$(A_1') \quad \frac{dn_1}{dt} = \varepsilon_1(1-n_2)n_1, \qquad (A_2') \quad \frac{dn_2}{dt} = -\varepsilon_2(1-n_1)n_2.$$

Multiplying these equations respectively by ε_2 and ε_1 and adding we have

$$[11] \qquad \frac{d}{dt}(\varepsilon_2 n_1 + \varepsilon_1 n_2) = \varepsilon_1\varepsilon_2(n_1-n_2).$$

Multiplying them respectively by $\frac{\varepsilon_2}{n_1}$ and $\frac{\varepsilon_1}{n_2}$, and adding, we find

$$\frac{\varepsilon_2}{n_1}\frac{dn_1}{dt} + \frac{\varepsilon_1}{n_2}\frac{dn_2}{dt} = \varepsilon_1\varepsilon_2(n_1-n_2),$$

that is to say

$$[12] \qquad \frac{d}{dt}(\log {n_1}^{\varepsilon_2} + \log {n_2}^{\varepsilon_1}) = \varepsilon_1\varepsilon_2(n_1-n_2).$$

Equating the first members of [11] and [12] there follows

$$\frac{d}{dt}(\varepsilon_2 n_1 + \varepsilon_1 n_2) = \frac{d}{dt}(\log {n_1}^{\varepsilon_2} + \log {n_2}^{\varepsilon_1}),$$

and integrating and passing from logarithms to numbers

$${n_1}^{\varepsilon_2}{n_2}^{\varepsilon_1} = Ce^{\varepsilon_2 n_1 + \varepsilon_1 n_2}$$

where C is a positive constant. Whence

[13] $$\left(\frac{n_1}{e^{n_1}}\right)^{\varepsilon_2} = C\left(\frac{n_2}{e^{n_2}}\right)^{-\varepsilon_1}.$$

From (A'_1) and (A'_2) it follows that

$$dt = \frac{dn_1}{\varepsilon_1(1-n_2)n_1} = \frac{dn_2}{-\varepsilon_2(1-n_1)n_2}.$$

If by means of the integral [13] we express n_2 in terms of n_1 or n_1 in terms of n_2 and substitute respectively these values in the preceding equations the variables remain separate, and the integration is reduced to a quadrature.

3. But we wish to examine directly the solution, and especially the integral [13].

Therefore let us place

[14] $$x = \left(\frac{n_1}{e^{n_1}}\right)^{\varepsilon_2} = C\left(\frac{n_2}{e^{n_2}}\right)^{-\varepsilon_1}$$

and let us consider the curve Γ_1, which has n_1 and x for abscissa and ordinate, and the curve Γ_2, which has n_2 and x for abscissa and ordinate (fig. 1).

We shall have

[15] $$\frac{d}{dn_1}\left(\frac{n_1}{e^{n_1}}\right) = e^{-n_1}(1-n_1)$$

which is positive for $n_1 < 1$ and negative for $n_1 > 1$. Then while n_1 varies between 0 and ∞, x increases from 0 to its maximum value $\left(\frac{1}{e}\right)^{\varepsilon_2}$ for $n_1 = 1$, and then approaches 0 as n_1 increases indefinitely. Whereas while n_2 varies between 0 and ∞, x decreases from ∞ to its minimum value Ce^{ε_1} for $n_2 = 1$, then increases without limit becoming ∞ for $n_2 = \infty$. The nature of the curves Γ_1 and Γ_2 appears then as shown in figure 1.

The constant C is determined from [13] whenever the initial values of n_1 and n_2 are known, and it is

$$C \leq e^{-(\varepsilon_1+\varepsilon_2)}.$$

If $C < e^{-(\varepsilon_1+\varepsilon_2)}$, that is if $e^{-\varepsilon_2} > Ce^{\varepsilon_1}$, for every value of x between Ce^{ε_1} and $e^{-\varepsilon_2}$ there correspond two values of n_1 and two of n_2, excluding the two values corresponding to the points C_1 and C_2 of maximum and minimum ordinates of the two curves Γ_1 and Γ_2. Having

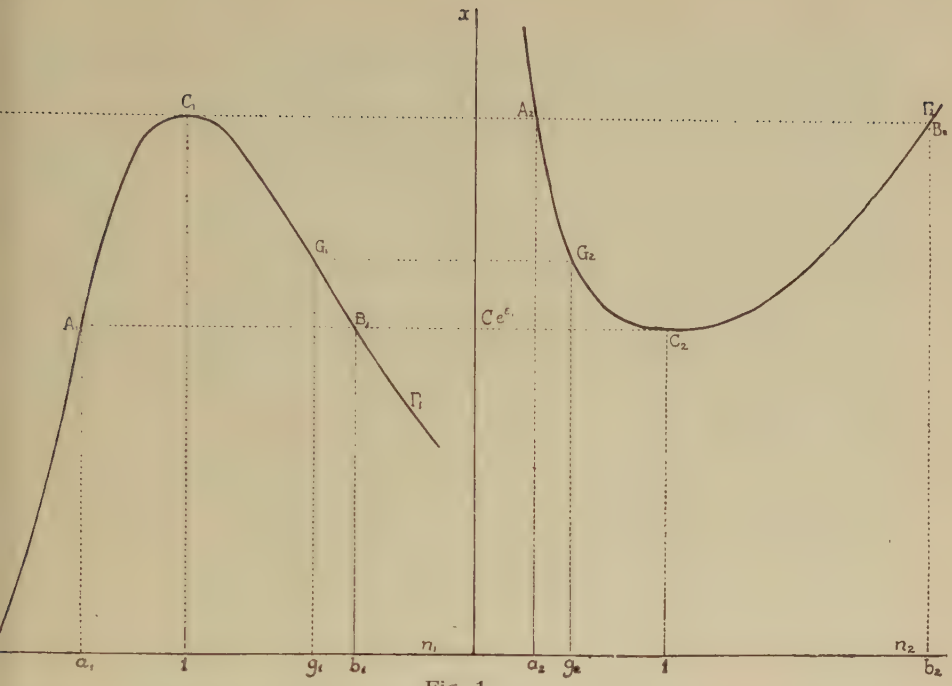

Fig. 1.

arranged the two curves as in fig. 1, with one axis of abscissas the continuation of the other, let us draw the normals to x from the vertices C_1 and C_2 and consider the sections $A_1C_1B_1$, $A_2C_2B_2$ of the two curves lying between these two parallels. Let $a_1 < 1$ and $b_1 > 1$ be the abscissas of A_1 and B_1, $a_2 < 1$, $b_2 > 1$ the abscissas of A_2 and B_2.

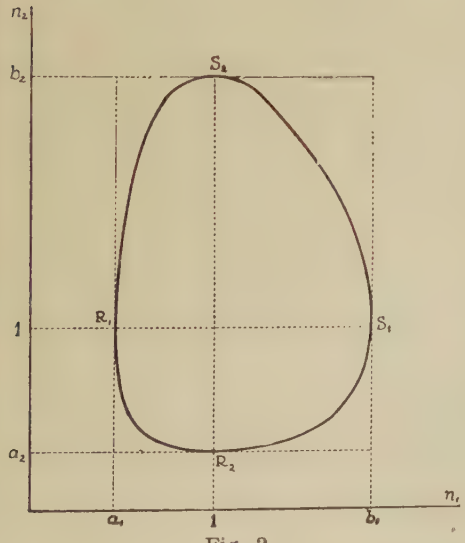

Fig. 2.

Then let us try to construct the curve λ having n_1 for abscissa and n_2 for ordinate. First let us make the point A_2 correspond to the point C_1 and trace the arc C_1B_1 with the point G_1. Then in the curve Γ_2 let us trace the arc A_2C_2, and, corresponding to G_1 on Γ_1 we shall have G_2 on Γ_2, on the same perpendicular to x. Then the value $n_2 = g_2$ will correspond to $n_1 = g_1$, g_1 and g_2 being respectively the abscissas of G_1 and G_2. Then while n_1 increases from 1 to b_1, n_2 will increase from a_2

to 1, that is the curve of figure 2 will be traced from the point R_2 of coordinates $(1, a_2)$ to the point S_1 of coordinates $(b_1, 1)$. Continuing, while n_1 decreases from b_1 to 1, n_2 will increase from 1 to b_2, that is we shall move in figure 2 from the point S_1 of coordinates $(b_1, 1)$ to the point S_2 of coordinates $(1, b_2)$; and as n_1 decreases from 1 to a_1, n_2 decreases from b_2 to 1, that is in figure 2 we move from point S_2 or coordinates $(1, b_2)$ to the point R_1 of coordinates $(a_1, 1)$. Finally when n_1 increases from a_1 to 1, n_2 will decrease from 1 to a_2 and in figure 2 we go from the point R_1 of coordinates $(a_1, 1)$ to the point R_2 of coordinates $(1, a_2)$.

On our return to the point of departure there begins again the periodic tracing of the closed cycle of figure 2, and by virtue of [14], (as follows also from figure 1), when n_1 and n_2 take again the same values x also takes the same value.

4. From [14] it follows that $\log x = \varepsilon_2 (\log n_1 - n_1)$, and then, taking the derivative with respect to t and using (A_1'),

$$\frac{1}{x}\frac{dx}{dt} = \varepsilon_2 \left(\frac{1}{n_1} - 1\right)\frac{dn_1}{dt} = \varepsilon_1 \varepsilon_2 (1 - n_1)(1 - n_2)$$

that is

$$dt = \frac{dx}{\varepsilon_1 \varepsilon_2 x (1 - n_1)(1 - n_2)}.$$

From which it follows that each time we trace with n_1 and n_2 the closed cycle of fig. 2, t will increase by a constant quantity T. From this it follows

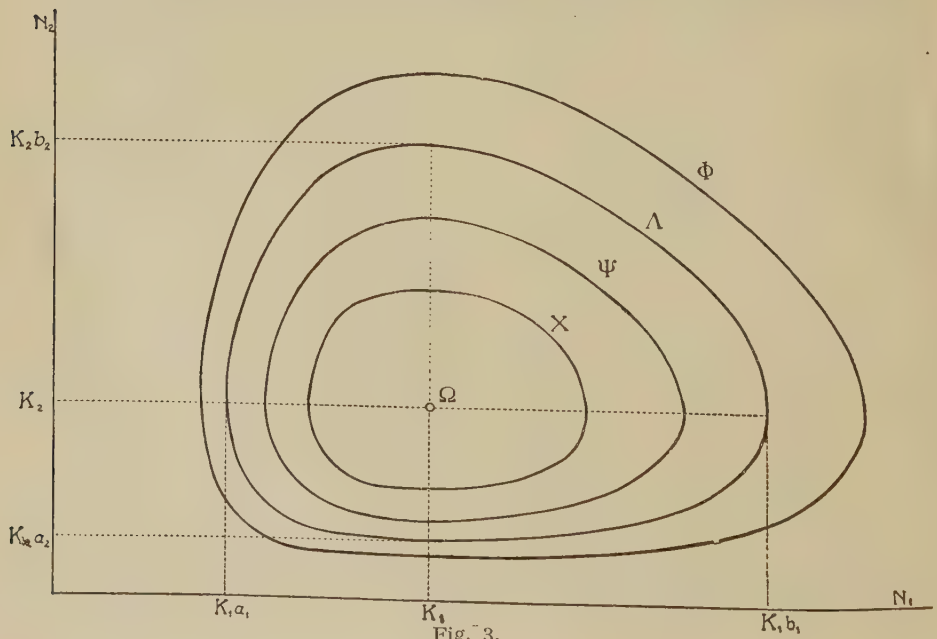

Fig. 3.

that n_1 and n_2, and by virtue of [10] also N_1 and N_2 will be periodic functions of the time, with the period T. The curve A of fig. 3 obtained from fig. 2 by multiplying the abscissas by K_1, and the ordinates by K_2, namely the curve which gives us the diagram of the cycle which relates N_1 to N_2 may be called the cycle of fluctuation and $K_1(b_1 - a_1)$, $K_2(b_2 - a_2)$ the amplitudes of the fluctuations of the two species. In general the cycle of fluctuation will not have a centre of symmetry, yet the point Ω whose coordinates are K_1 and K_2 stands inside all the possible cycles of fluctuation Φ, A, Ψ, X, ... dependent upon all the possible initial conditions of the two species as is indicated in fig. 3. The name centre of fluctuation may be given then to the point Ω. All the curves of diagram 3 will be obtained by keeping ε_1, ε_2, γ_1, γ_2 constant and letting the constant C take different values. These curves do not meet each other, but lie one within the other.

We have then in this case a periodic fluctuation of the number of individuals of the two species, with period T, or the phenomenon will have a cyclically periodic character.

Let us represent the fluctuation of n_1 and n_2 as functions of the time and we shall have figure 4.

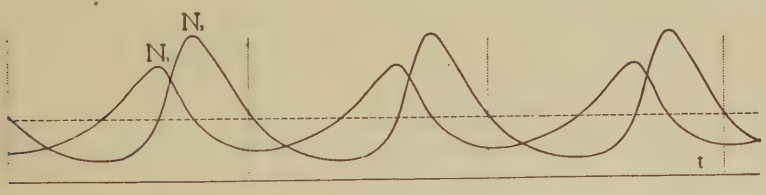

Fig. 4.

5. To determine the period T we shall need to calculate the integral

$$\int \frac{dx}{\varepsilon_1 \varepsilon_2 x (1-n_1)(1-n_2)}$$

extending it in succession over the four arcs R_2S_1, S_1S_2, S_2R_1, R_1R_2.

The sum of the four integrals will give us the period T.

The function under the integral sign becomes infinite at the four vertices R_1, R_2, S_1, S_2, but as is easily recognized, the order of infinitude is such that the integrals are convergent.

The preceding integral proves that the period T depends only on ε_1, ε_2 and C.

In the following section we shall calculate approximately this period, assuming that the fluctuations are small[1]).

6. The approximate case in which the fluctuations are small can be treated easily by starting with equations (A_1) and (A_2).

In fact placing

[16] $$n_1 = 1 + v_1, \qquad n_2 = 1 + v_2$$

we shall have

[17] $$N_1 = K_1(1 + v_1), \qquad N_2 = K_2(1 + v_2).$$

Equations (A_1'), (A_2') will become

$$(A_1'') \quad \frac{dv_1}{dt} = -\varepsilon_1 v_2 - \varepsilon_1 v_1 v_2, \qquad (A_2'') \quad \frac{dv_2}{dt} = \varepsilon_2 v_1 + \varepsilon_2 v_1 v_2.$$

If the fluctuations are small v_1 and v_2 can be considered as small quantities of the 1st order, whence, if we neglect all terms of the 2nd order in the preceding equations, we shall have

$$\frac{dv_1}{dt} = -\varepsilon_1 v_2, \qquad \frac{dv_2}{dt} = \varepsilon_2 v_1$$

which are integrated by the formulas

$$v_1 = L\sqrt{\varepsilon_1}\cos\left(\sqrt{\varepsilon_1\varepsilon_2}\,t + a\right), \qquad v_2 = L\sqrt{\varepsilon_2}\sin\left(\sqrt{\varepsilon_1\varepsilon_2}\,t + a\right)$$

where L and a are both constants.

We shall have then, by using equations [8], [10], [16] and placing

$$L\frac{\varepsilon_1\varepsilon_2}{\gamma_1\gamma_2} = E,$$

[18]
$$N_1 = \frac{\varepsilon_2}{\gamma_2} + \frac{\gamma_1}{\sqrt{\varepsilon_1}}E\cos\left(\sqrt{\varepsilon_1\varepsilon_2}\,t + a\right)$$

$$N_2 = \frac{\varepsilon_1}{\gamma_1} + \frac{\gamma_2}{\sqrt{\varepsilon_2}}E\sin\left(\sqrt{\varepsilon_1\varepsilon_2}\,t + a\right)$$

whence N_1 and N_2 appear periodic with the period $\frac{2\pi}{\sqrt{\varepsilon_1\varepsilon_2}}$.

We should have arrived at this same value by calculating directly

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[1]) For the exact calculation of the period T, I refer to the article already cited, "Memoria della R. Accademia dei Lincei". Part 1st, § 3, No. 5.

the integral T of the preceding section and neglecting terms of infinitesimal order.

We can assume then that the period of the cycle of fluctuations of the two species is given approximately by

$$T = \frac{2\pi}{\sqrt{\varepsilon_1 \varepsilon_2}}.$$

If, as in article 2, we call t_1 and t_2 the two times in which respectively the first species doubles itself and the other is reduced by half, we shall have

$$T = \frac{2\pi \sqrt{t_1 t_2}}{0.693} = 9.06 \sqrt{t_1 t_2}.$$

The cycle of fluctuation will become an ellipse having its centre at the centre of fluctuation and having for semiaxes

$$E \frac{\gamma_1}{\sqrt{\varepsilon_1}}, \qquad E \frac{\gamma_2}{\sqrt{\varepsilon_2}}$$

whence the amplitudes of the fluctuations will be

$$f_1 = 2E \frac{\gamma_1}{\sqrt{\varepsilon_1}}, \qquad f_2 = 2E \frac{\gamma_2}{\sqrt{\varepsilon_2}}.$$

The ratio of the amplitudes of the two fluctuations will be

$$\frac{f_1}{f_2} = \frac{\gamma_1}{\gamma_2} \sqrt{\frac{\varepsilon_2}{\varepsilon_1}}.$$

The family of cycles of fluctuation will in this case consist of a group of homothetical ellipses having for common centre the centre of fluctuation. (See fig. 5.)

7. Now let us consider the average number of individuals of the two species during a cycle.

For that let us take equations (A'_1), (A'_2). Dividing both members respectively by n_1 and n_2 we shall have

$$\frac{d \log n_1}{dt} = \varepsilon_1 (1 - n_2), \qquad \frac{d \log n_2}{dt} = -\varepsilon_2 (1 - n_1),$$

and integrating between the times t' and t'' at which times n_1 and n_2 assume respectively the values n_1', n_1''; n_2', n_2'', the following equations will be obtained:

$$\log \frac{n_1''}{n_1'} = \varepsilon_1 \left[(t''-t') - \int_{t'}^{t''} n_2 \, dt \right], \qquad \log \frac{n_2''}{n_2'} = -\varepsilon_2 \left[(t''-t') - \int_{t'}^{t''} n_1 \, dt \right].$$

If we extend the integrals to a period T the first members vanish and we have

$$T = \int_0^T n_1 \, dt = \int_0^T n_2 dt$$

which is equivalent to saying

$$\frac{1}{T} \int_0^T n_1 dt = \frac{1}{T} \int_0^T n_2 dt = 1 .$$

Then the averages of the values of n_1 and n_2 in a period are equal to 1 and by [10]

$$\frac{1}{T} \int_0^T N_1 dt = K_1 = \frac{\varepsilon_2}{\gamma_2}, \qquad \frac{1}{T} \int_0^T N_2 dt = K_2 = \frac{\varepsilon_1}{\gamma_1},$$

that is the coordinates of the centre of fluctuation are the average values of the numbers of individuals of the species during a cycle. From this it follows that if ε_1, ε_2, γ_1, γ_2 stay constant, the averages of the individuals of the two species during a cycle of fluctuation will always be the same whatever may be the initial numbers of individuals of the two species.

Let us see how these averages change with variation of ε_1 and ε_2, supposing γ_1 and γ_2 constants. It is seen at once that the average of the first species increases in proportion with ε_2, and that of the second species decreases in proportion with ε_1 so long as this quantity remains positive. Now to make ε_2 increase means destroying uniformly individuals of the second species in a quantity proportional to their number, and to make ε_1 decrease means destroying uniformly individuals of the first species in a quantity proportional to their number; from which it follows that if we try to contemporaneously destroy individuals of both species in the aforesaid manner but always keeping ε_1 positive, there will be an increase in the average of the individuals of the first species (those fed upon) while there will be a decrease in the average of the individuals of the second species (those feeding upon others). In figure 6 we have

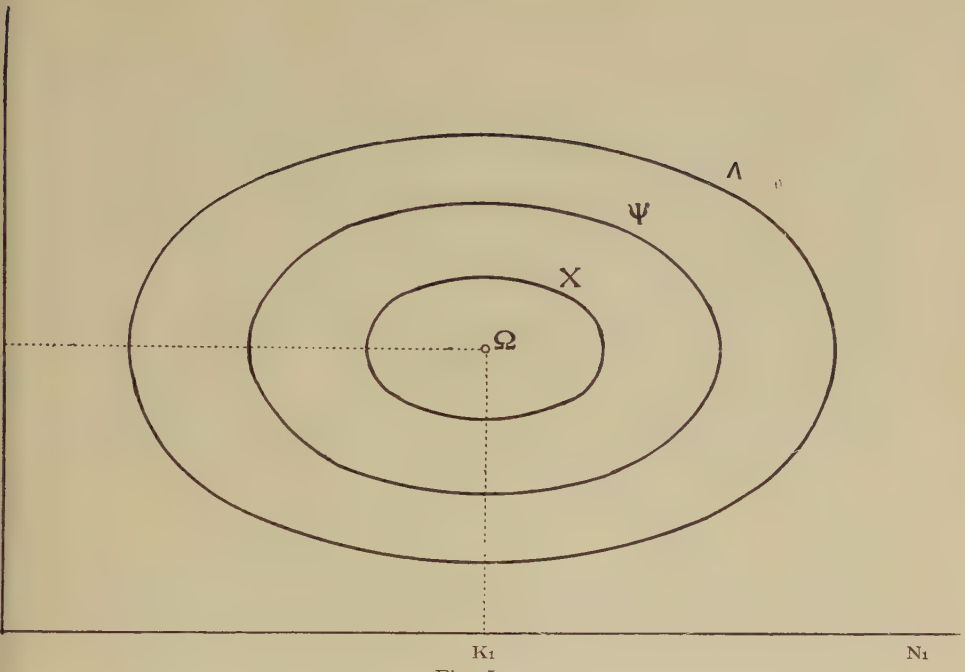

Fig. 5.

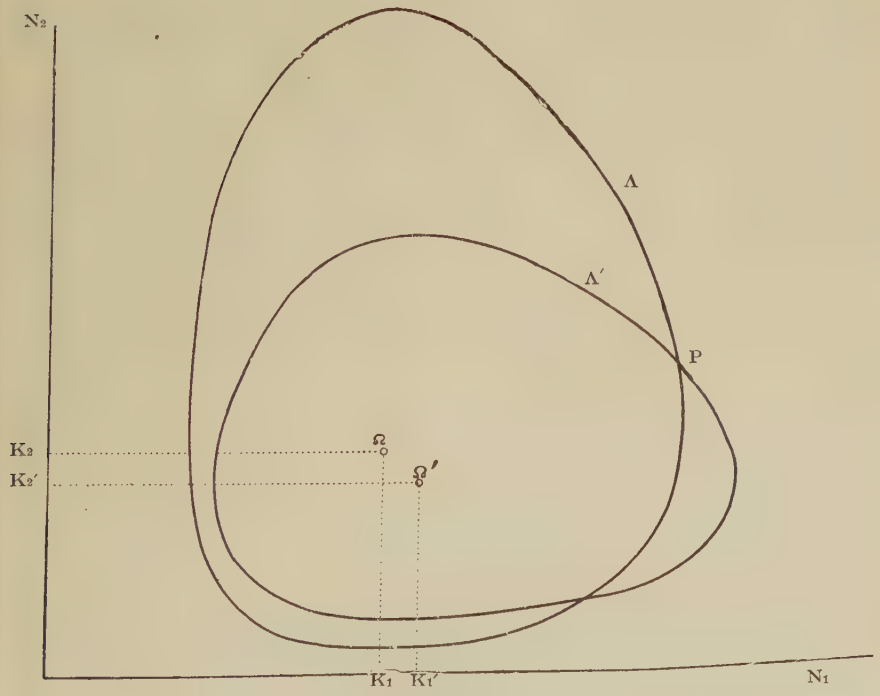

Fig. 6.

represented the transition from a cycle $\mathcal{A}$ corresponding to the parameters ε_1 and ε_2 to a cycle $\mathcal{A}'$ corresponding to parameters $\varepsilon_1' < \varepsilon_1$, $\varepsilon_2' > \varepsilon_2$ (the parameters γ_1 and γ_2 are supposed invariable and $\varepsilon_1' > 0$). We may conceive of this transition as occurring in an instant corresponding to the point P of intersection of the two cycles, that is to say, without having any sensible change at that instant in the number of the individuals of the two species, although a change is disclosed with the passage of time by virtue of the constant action due to the variation of the parameters ε_1 and ε_2. The centre Ω' of $\mathcal{A}'$ is moved to the right of and below Ω which indicates a diminution in the average value of N_2 and an increase in the average value of N_1.

To increase the protection of the species that is eaten from the voracity of the other means to diminish γ_1 and γ_2 and this corresponds to an increase in the average quantity of the two species.

8. We can sum up the various results obtained in the following laws which we shall call the fundamental laws of the fluctuations of the two species living together:

1st) **Law of the periodic cycle.** The fluctuations of the two species are periodic and the period depends only upon ε_1, ε_2 and C, (namely upon the coefficients of increase and decrease and the initial conditions).

2nd) **Law of the conservation of the averages.** The averages of the numbers of individuals of the two species are constant whatever may be the initial values of the numbers of individuals of the two species just so long as the coefficients of increase and decrease of the two species and those of protection and of offense (ε_1, ε_2, γ_1, γ_2) remain constant.

3rd) **Law of the disturbance of the averages.** If an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the average of the number of individuals of the species that is eaten increases and that of the individuals of the species feeding upon the other diminishes[1]).

Increasing the protection of the species fed upon increases, however, both the averages.

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[1]) It is understood that this law is valid within certain limits as is explicitly said in N. 7, that is as long as the coefficient of increase ε_1 remains positive. In § 5 a special study will be made of the limit within which an element destructive of two species assists the species that is eaten.

In the case in which the fluctuations are small, we have the following approximate laws:

1st) The small fluctuations are isocronous, that is to say their period is not affected perceptibly either by the initial number of individuals or by the conditions of protection and offense.

2nd) The period of fluctuation is proportional to the geometric mean of the times in which the first species, alone, would double itself and the second, by itself, would be reduced by half. ($T = 9.06\sqrt{t_1 t_2}$).

3rd) The uniform destruction of individuals of the species feeding upon the other accelerates the fluctuations, and the destruction of individuals of the species eaten retards them.

If the individuals of the two species are destroyed, contemporaneously and uniformly, the ratio of the amplitude of the fluctuation of the species eaten to the amplitude of the fluctuation of the species feeding upon the other increases.

It seems that the animal species for which in their natural state the verifications of these laws can most easily be carried out are fish, of which there are in fact species which feed upon others. Continual fishing constitutes a uniform destruction of individuals of the various species.

The cessation of fishing during the period of the recent war and its resumption after the war established transitions comparable to those considered above, from one cycle to another. Besides, the greater or less abundance of fish of various species determined by statistics gives a measure of the abundance of the individuals of the various species; hence the statistics of fishery furnish data on the fluctuations.

The results of the statistics are seen to be in accord with the mathematical predictions[1]).

[1]) Cf. the note for the 1st section Page 2, in which the statistics of Doctor D'Ancona are spoken of.

Charles Darwin had an intuition of the phenomena connected with the law of disturbance of averages, when, speaking of the struggle for life, he said:

"The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals which determines the average numbers of a species.Thus, there seems to be little doubt that the stock of partridges, grouse and hares on any large estate depends chiefly on the destruction of vermin. If not one head of game were shot during the next twenty years in England, and, at the same time, if no ver-

§ 4. Effects of the Various Actions which two Species living together can have on each other.

1. Let us suppose we have two species living together, and let N_1 and N_2 be respectively the numbers of individuals in each. The number of encounters of individuals of the first species with those of the second species, which occur in a unit of time, will be proportional to $N_1 N_2$ and can therefore be assumed equal to $\alpha N_1 N_2$, α being a constant. Let λ_1 and λ_2 be the coefficients of increase, positive or negative, of the two species when each is alone. In the case which we have already treated λ_1 is positive and λ_2 is negative. Moreover these meetings are unfavorable to the first species (the species fed upon), while they are favorable to the second species (the species feeding upon the other). Let us indicate by β_1 the increase of individuals of the first species and by β_2 the increase of individuals of the second species due to a certain number of encounters, for example n. In the preceding case β_1 would have to be taken negative and β_2 positive. In the time dt the increases of the two species will be respectively

$$dN_1 = \lambda_1 N_1 dt + \frac{\beta_1}{n} \alpha N_2 N_1 dt,$$

$$dN_2 = \lambda_2 N_2 dt + \frac{\beta_2}{n} \alpha N_1 N_2 dt.$$

Using

$$\frac{\beta_1}{n} \alpha = \mu_1, \qquad \frac{\beta_2}{n} \alpha = \mu_2$$

the preceding equations will become

[19]
$$\begin{cases} \dfrac{dN_1}{dt} = N_1 (\lambda_1 + \mu_1 N_2) \\ \dfrac{dN_2}{dt} = N_2 (\lambda_2 + \mu_2 N_1) \end{cases}$$

and if we make evident the signs which are given in the preceding case, writing

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min were destroyed, there would, in all probability, be less game than at present, although hundreds of thousands of game animals are now annually shot."

Charles Darwin, The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. Sixth edition, with corrections to 1871. London, John Murray, 1882 (pp. 53—54).

$$\lambda_1 = \varepsilon_1 \qquad \lambda_2 = -\varepsilon_2$$
$$\mu_1 = -\gamma_1 \qquad \mu_2 = \gamma_2$$

we arrive again at the equations (A_1) and (A_2) of section 3, namely

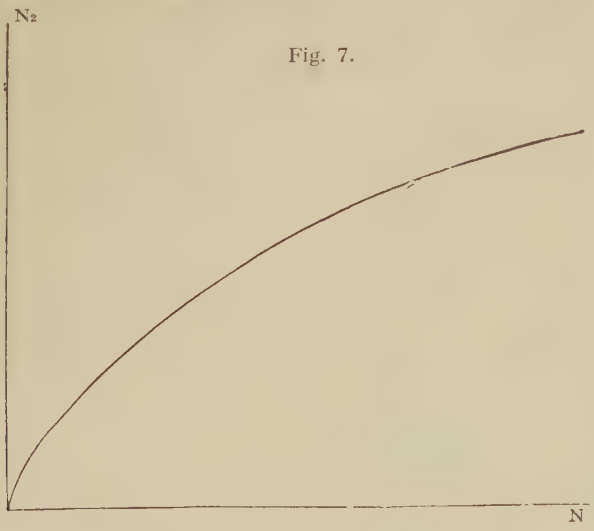
$$\frac{dN_1}{dt} = N_1 (\varepsilon_1 - \gamma_1 N_2)$$

$$\frac{dN_2}{dt} = N_2 (-\varepsilon_2 + \gamma_2 N_1).$$

Thus appears a justification (as mentioned in N. 1 of § 3) of the assumption that the coefficients of increase are linear with respect to N_2 and N_1.

2. Let us now take equations [19] without concerning ourselves with the signs of the coefficients, that is admitting that they may be positive or negative; we may assume that they represent the laws of increase of two species living together for which λ_1 and λ_2 are the coefficients of increase, while μ_1 and μ_2 are the coefficients of increase depending on encounters. The signs of λ_1 and λ_2 tell us if the species are increasing or decreasing by themselves, while the signs of the coefficients μ_1 and μ_2 indicate whether the encounters are favorable or unfavorable to one species and to the other respectively. For example if λ_1 and λ_2 are positive and μ_1, μ_2 are negative this will show that the species are increasing by themselves, and that the encounters are unfavorable to both species. We shall consider all possible cases, making all possible combinations of these coefficients taking them positive or negative. According to the signs of λ_1, μ_1, λ_2, μ_2 the different cases relating to equations [19] are represented in the following figures:

Fig. 7.



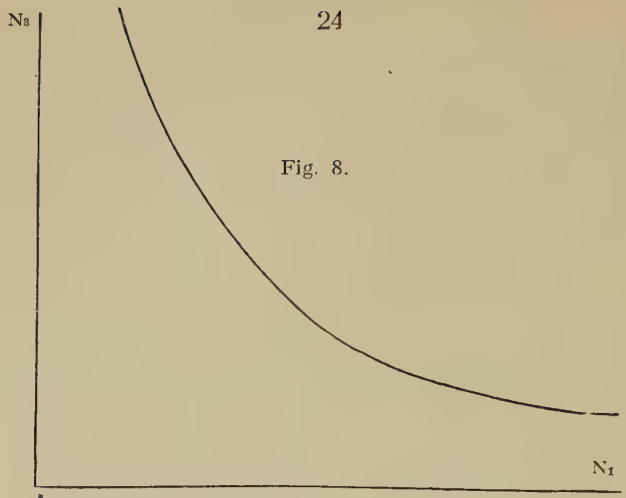


Fig. 8.

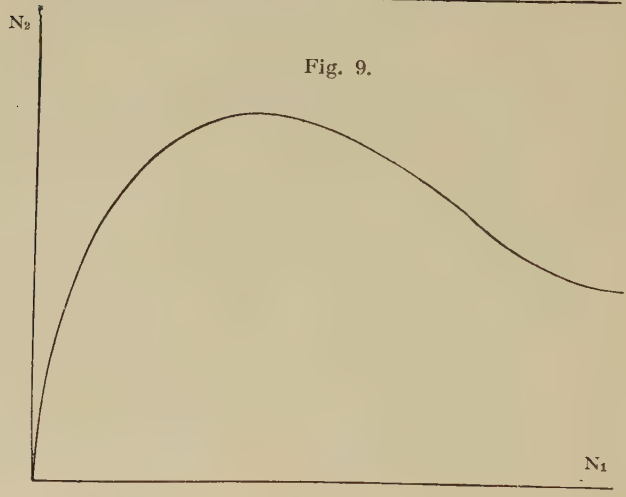


Fig. 9.

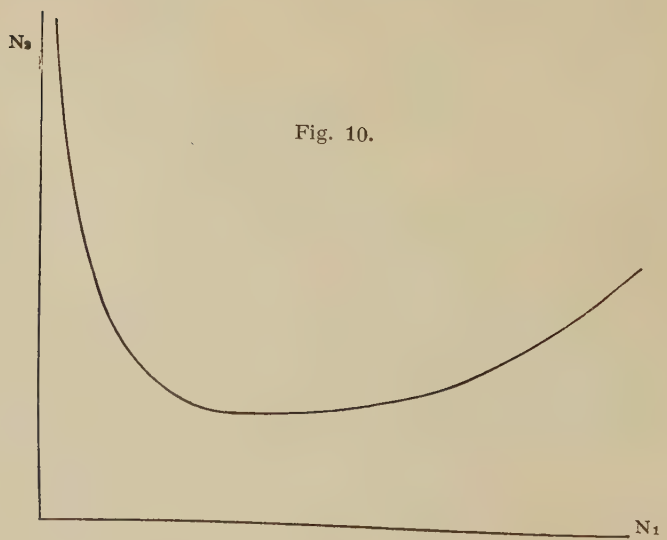


Fig. 10.

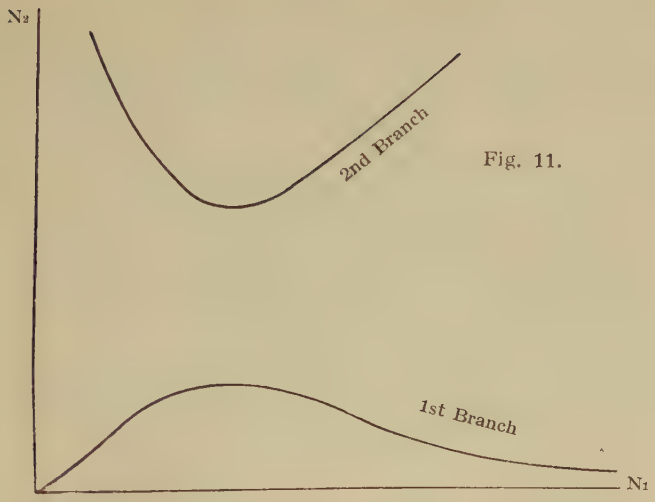


Fig. 11.

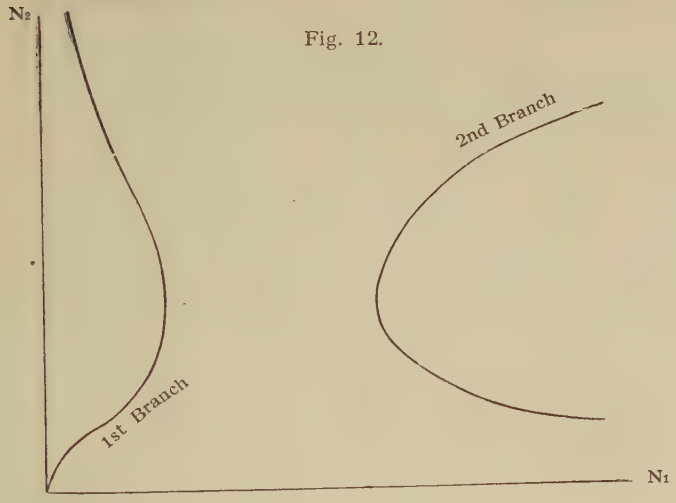


Fig. 12.

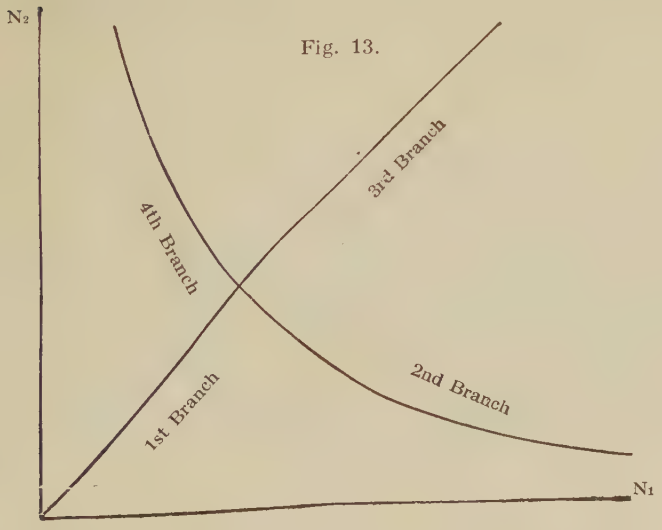


Fig. 13.

The following table indicates which cases correspond to the preceding figures.

$$\left.\begin{array}{l}\lambda_1 > 0,\ \mu_1 > 0,\ \lambda_2 > 0,\ \mu_2 > 0,\\ \lambda_1 < 0,\ \mu_1 < 0,\ \lambda_2 < 0,\ \mu_2 < 0,\end{array}\right\} \text{ fig. 7} \begin{cases}\text{l. r.}\\ \text{r. l.}\end{cases}$$

$$\left.\begin{array}{l}\lambda_1 < 0,\ \mu_1 < 0,\ \lambda_2 > 0,\ \mu_2 > 0,\\ \lambda_1 > 0,\ \mu_1 > 0,\ \lambda_2 < 0,\ \mu_2 < 0,\end{array}\right\} \text{ fig. 8} \begin{cases}\text{r. l.}\\ \text{l. r.}\end{cases}$$

$$\left.\begin{array}{l}\lambda_1 > 0,\ \mu_1 > 0,\ \lambda_2 > 0,\ \mu_2 < 0,\\ \lambda_1 < 0,\ \mu_1 < 0,\ \lambda_2 < 0,\ \mu_2 > 0,\end{array}\right\} \text{ fig. 9} \begin{cases}\text{l. r.}\\ \text{r. l.}\end{cases}$$

$$\left.\begin{array}{l}\lambda_1 < 0,\ \mu_1 < 0,\ \lambda_2 > 0,\ \mu_2 < 0,\\ \lambda_1 > 0,\ \mu_1 > 0,\ \lambda_2 < 0,\ \mu_2 > 0,\end{array}\right\} \text{ fig. 10} \begin{cases}\text{r. l.}\\ \text{l. r.}\end{cases}$$

$$\left.\begin{array}{l}\lambda_1 > 0,\ \mu_1 < 0,\ \lambda_2 > 0,\ \mu_2 < 0,\\ \lambda_1 < 0,\ \mu_1 > 0,\ \lambda_2 < 0,\ \mu_2 > 0,\end{array}\right\} \text{ fig. 11} \begin{cases}\begin{cases}\text{l. r. 1st branch}\\ \text{r. l. 2nd branch}\end{cases}\\ \begin{cases}\text{r. l. 1st branch}\\ \text{l. r. 2nd branch}\end{cases}\end{cases}$$

$$\left.\begin{array}{l}\lambda_1 > 0,\ \mu_1 < 0,\ \lambda_2 > 0,\ \mu_2 < 0,\\ \lambda_1 < 0,\ \mu_1 > 0,\ \lambda_2 < 0,\ \mu_2 > 0,\end{array}\right\} \text{ fig. 12} \begin{cases}\begin{cases}\text{u. 1st branch}\\ \text{d. 2nd branch}\end{cases}\\ \begin{cases}\text{d. 1st branch}\\ \text{u. 2nd branch}\end{cases}\end{cases}$$

$$\left.\begin{array}{l}\lambda_1 > 0,\ \mu_1 < 0,\ \lambda_2 > 0,\ \mu_2 < 0,\\ \lambda_1 < 0,\ \mu_1 > 0,\ \lambda_2 < 0,\ \mu_2 > 0,\end{array}\right\} \text{ fig. 13} \begin{cases}\begin{cases}\text{l. r. 1st branch, 2nd branch}\\ \text{r. l. 3rd branch, 4th branch}\end{cases}\\ \begin{cases}\text{r. l. 1st branch, 2nd branch}\\ \text{l. r. 3rd branch, 4th branch}\end{cases}\end{cases}$$

In the preceding table *l. r.* signifies that with increase in time the curve is traced from left to right, *r. l.* from right to left, *d.* downward and *u.* upward.

§ 5. Limits within which a Cause destructive of two Species favors the Species fed upon.

1. We have shown (§ 3, N. 7) that decreasing ε_1, namely the coefficient of increase of the species fed upon, and increasing ε_2, or the coefficient of decrease of the species feeding upon the other, causes an increase in the average of the individuals of the first species and diminishes that of the second species, from which we have enunciated in N. 8 the law: If an attempt is made to destroy the individuals of the two species uniformly and in proportion to their number, the

average of the number of individuals of the species that is eaten increases, and that of the individuals of the species feeding upon the other diminishes.

But we have added that this law is valid within certain limits, that is as long as ε_1 stays positive.

2. We shall now conduct a study of the behavior of the phenomenon in detail. Let us denote by $\alpha\lambda$ the ratio between the number n_1 of individuals of the first species which are consumed, that is which are subtracted from the biological association, in the unit of time, and the total number of individuals in it, and by $\beta\lambda$ the analogous ratio for the second species. During the time dt there are lost from the biological association respectively

$$n_1 dt = \alpha\lambda N_1 dt \qquad \text{and} \qquad n_2 dt = \beta\lambda N_2 dt$$

individuals of the two species, wherefore the equations (A_1), (A_2) must be modified by substituting in them for ε_1 and ε_2 respectively

$$\varepsilon_1 - \alpha\lambda, \qquad\qquad \varepsilon_2 + \beta\lambda.$$

The anharmonic ratio of the four numbers n_2, N_2, n_1, N_1, that is

$$(n_2 : N_2) : (n_1 : N_1) = \frac{\beta}{\alpha} = \delta,$$

gives the ratio of the percentages of destruction or subtraction for the two species, which can be supposed to depend solely upon the way in which this destruction or subtraction occurs, while the intensity of the destruction or subtraction can be made to depend upon λ. Increasing λ then, while α and β remain constant, will have the significance of intensifying the subtraction if the same means of carrying it out is always used, while changing the ratio $\delta = \frac{\beta}{\alpha}$ means altering the mode of procedure through which the destruction or subtraction occurs.

To refer to a concrete example, let us consider two species of fish living together, the second of which feeds on the first. Increasing λ without varying either α or β means intensifying the fishing, always employing the same method of fishing, while changing $\delta = \frac{\beta}{\alpha}$ means changing the method of fishing.

3. The equations (A_1) and (A_2) will become then

[20] $$\frac{dN_1}{dt} = (\varepsilon_1 - \alpha\lambda - \gamma_1 N_2) N_1$$

[20'] $$\frac{dN_2}{dt} = (-\varepsilon_2 - \beta\lambda + \gamma_2 N_1) N_2 .$$

If $\varepsilon_1' = \varepsilon_1 - \alpha\lambda > 0$ the fluctuation will occur with a period T (§ 3, N. 4). The number of individuals of the first species subtracted in the time dt will be

$$\alpha\lambda N_1 dt,$$

and during the period T

$$\int_o^T \alpha\lambda N_1 dt ,$$

whence the average of individuals subtracted in the unit of time will be

$$P = \frac{1}{T}\int_o^T \alpha\lambda N_1 dt = \frac{\alpha\lambda}{T}\int_o^T N_1 dt .$$

But since from § 3, N. 7

$$\frac{1}{T}\int_o^T N_1 dt = \frac{\varepsilon_2 + \beta\lambda}{\gamma_2} = \frac{\varepsilon_2'}{\gamma_2},$$

we have

$$P = \frac{\alpha\lambda\,(\varepsilon_2 + \beta\lambda)}{\gamma_2} .$$

As $\varepsilon_1 - \alpha\lambda > 0$, the upper limit of λ will be $\frac{\varepsilon_1}{\alpha}$ and consequently the upper limit of P will be

$$P_m = \frac{\varepsilon_1\,(\varepsilon_2 + \delta\varepsilon_1)}{\gamma_2} .$$

If we refer to the concrete example of fishing, we may conclude that, if the same method of fishing is maintained (that is if δ is constant), the average quantity of the first species, caught in the unit of time, during a cycle of fluctuation, can not exceed P_m, though it may approach this number as closely as we please.

Also we may say that P_m will be greater according as the harmonic ratio δ is greater.

4. If λ exceeds the value $\frac{\varepsilon_1}{\alpha}$ so that

$$\varepsilon_1 - \alpha\lambda < 0,$$

then the fluctuation will cease to exist, both the species will tend to disappear (see § 4) and we shall have the case denoted in § 4 with the type represented in figure 9 in which the curve is to be read from right to left.

It is interesting to examine the boundary case in which λ attains the value $\frac{\varepsilon_1}{\alpha}$. We arrive then at the point of transition from the type represented in fig. 2 to the type represented in fig. 9. As indicated in § 4, we have not considered the several cases of transition among the various types; but we shall examine this now because the subject which we are now treating requires it. It can serve as an example of the treatment of the various cases of transition from one type to another.

If $\lambda = \frac{\varepsilon_1}{\alpha}$ the equations [20], [20′] become

[21] $$\frac{dN_1}{dt} = -\gamma_1 N_1 N_2,$$

[21′] $$\frac{dN_2}{dt} = (-\varepsilon_2'' + \gamma_2 N_1) N_2,$$

where

$$\varepsilon_2'' = \varepsilon_2 + \varepsilon_1 \delta.$$

These equations have the integral

[22] $$N_1^{\varepsilon_2''} e^{-\gamma_2 N_1} = C e^{\gamma_1 N_2},$$

where C is a positive constant.

Letting

$$x = N_1^{\varepsilon_2''} e^{-\gamma_2 N_1} = C e^{\gamma_1 N_2}$$

the two curves Γ_1 and Γ_2 which have (N_1, x) and (N_2, x) respectively for abscissa and ordinate are represented in figure 14, whence employing the same mode of procedure which was followed in § 3, N. 3, (cf. fig. 1 and fig. 2) we can draw the curve which has [22] for its equation. (See fig. 15.)

The minimum and maximum values a_1, b_1 of N_1 will give the two real roots of the equation

[22′] $$N_1^{\varepsilon_2''} e^{-\gamma_2 N_1} = C.$$

When $\varepsilon_1' = \varepsilon_1 - \alpha\lambda$ becomes 0, the cyclical curves of fig. 3 assume, at the limit, the form of the curve of fig. 15. The lower part of the former

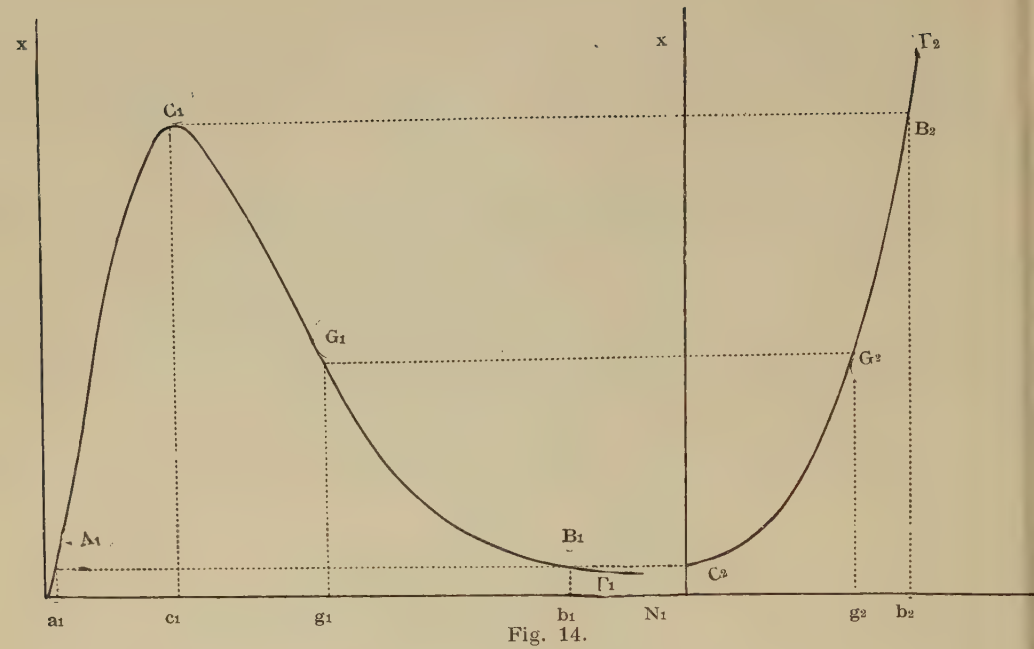


Fig. 14.

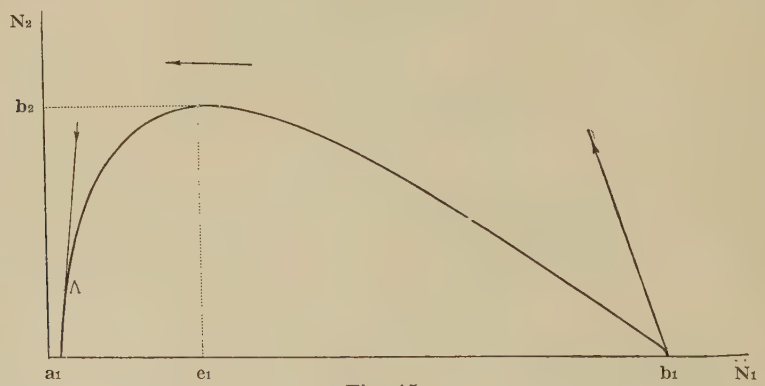


Fig. 15.

curves approaches the straight line segment $a_1 b_1$ of fig. 15. But while the curves of fig. 3 are traced clear around periodically, which constitutes the phenomenon of fluctuation, the line segment $a_1 b_1$ can never be traced because an infinite period of time is necessary for reaching the point a_1. Then any point whatever on the straight line $a_1 b_1$ corresponds to N_1 constant and $N_2 = 0$.

In fig. 16 three curves are represented, I, II, III, which issue from the same point P. Their respective equations are

$$\text{I.} \qquad N_1^{\varepsilon_2'}\ e^{-\gamma_2 N_1} = C' N_2^{-\varepsilon_1'}\ e^{\gamma_1 N_2}$$

$$\text{II.} \qquad N_1^{\varepsilon_2''}\ e^{-\gamma_2 N_1} = C'' e^{\gamma_1 N_2}$$

$$\text{III.} \qquad N_1^{\varepsilon_2'''}\ e^{-\gamma_2 N_1} = C''' N_2^{h} e^{\gamma_1 N_2}.$$

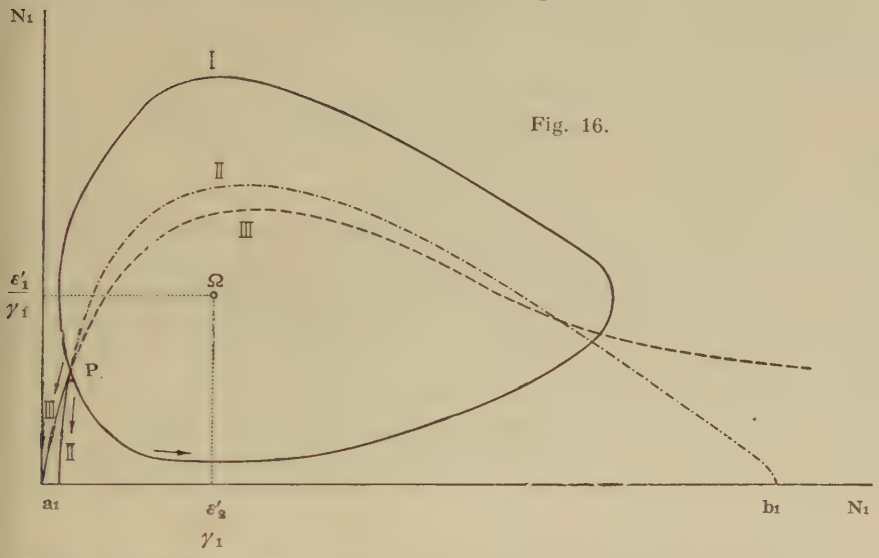


Fig. 16.

No. I is a curve of fluctuation which therefore corresponds to $\varepsilon_1' > 0$ (for this reason it is of the type of those in fig. 2), No. II is a curve of the type of those in fig. 15 (curve of transition from the type in fig. 2 to the type of fig. 9), No. III is a curve of the type of those in fig. 9 and corresponds to $\varepsilon_1 - \alpha\lambda$ negative and equal to $-h$. We have besides

$$0 < \varepsilon_2' < \varepsilon_2'' < \varepsilon_2'''.$$

The curves mentioned refer respectively to the three cases in which the intensity of destruction of the species does not attain the limit $\frac{\varepsilon_1}{\alpha}$, or is equal to it, or exceeds it.

§ 6. The Case of any Number whatever of Species which contend for the same Food.

1. It is easy to extend what has been done in the case of two species living together, which contend for the same food, to the case of any number of species.

Let us take the number of species to be n and let us assume $\varepsilon_1, \varepsilon_2, \ldots, \varepsilon_n$ to be the coefficients of increase which each species would have if alone.

Let us denote by $F(N_1, N_2, \ldots, N_n)\, dt$ the diminution in the quantity of food in the time dt, when the numbers of individuals of the different species are respectively $N_1, N_2, \ldots, N_n$. This function will be zero for $N_1 = N_2 = \ldots . N_n = 0$; it will be positive and increasing and will increase indefinitely with an indefinite increase in each N_r. For simplicity we could take F linear, that is

$$F(N_1, N_2, \ldots, N_n) = \alpha_1 N_1 + \alpha_2 N_2 + \ldots . + \alpha_n N_n$$

where the coefficients α_r are positive. But we shall leave F general.

The presence of N_1 individuals of the first species, of N_2 of the second, etc. will influence the coefficients of increase reducing ε_r to $\varepsilon_r - \gamma_r F(N_1, \ldots, N_n)$ where the positive coefficient γ_r measures the influence which the diminution of the food has upon the increase of the species.

We shall have then the differential equations

$$[23] \qquad \frac{dN_r}{dt} = N_r\,(\varepsilon_r - \gamma_r F(N_1, \ldots, N_n)), \qquad (r = 1, 2, \ldots, n)$$

from which follows

$$\frac{1}{\gamma_r N_r}\frac{dN_r}{dt} - \frac{1}{\gamma_s N_s}\frac{dN_s}{dt} = \frac{\varepsilon_r}{\gamma_r} - \frac{\varepsilon_s}{\gamma_s}$$

and integrating and passing from logarithms to numbers

$$\frac{N_r^{\frac{1}{\gamma_r}}}{N_s^{\frac{1}{\gamma_s}}} = Ce^{\left(\frac{\varepsilon_r}{\gamma_r} - \frac{\varepsilon_s}{\gamma_s}\right)t}$$

where C is a positive constant.

2. Let us arrange the ratios $\frac{\varepsilon_r}{\gamma_r}$ in order of size, that is let us suppose[1])

$$\frac{\varepsilon_1}{\gamma_1} > \frac{\varepsilon_2}{\gamma_2} > \frac{\varepsilon_3}{\gamma_3} > \ldots\ldots\ldots > \frac{\varepsilon_n}{\gamma_n},$$

then we shall have, if $r < s$

[1]) Let us exclude the cases of equality as of infinitesimally small probability.

$$\lim_{t=\infty} \frac{N_r^{\gamma_r}}{N_s^{\gamma_s}} = \infty .$$

As a consequence of this result either N_r can, with increase of time, take values as large as we please, or

$$\lim_{t=\infty} N_s = 0.$$

But the first case is to be excluded, because F increases indefinitely with indefinite increase of N_r, therefore in [23] the second member becomes negative when N_r exceeds a certain limit; whence the upper limit of N_r is finite. Then the second case must hold. From this it follows that all the species tend to disappear except the first.

To have the asymptotic variation of N_1 it will suffice to repeat what has been done in the case of two species alone.

§ 7. Case of any Number whatever of Species some of which feed upon others.

1. Let us consider the case of n species and let us suppose that the encounter of two individuals of different species always carries a result favorable to the species to which one belongs, and unfavorable to that to which the other belongs, or else a zero result for both. If N_r is the number of individuals of the species r and N_s the number of individuals of the species s the probability of an encounter of an individual of one with an individual of the other will be proportional to $N_r N_s$ whence we can assume that the number of encounters which take place in the unit of time is equal to $m_{rs} N_r N_s$. Let us suppose that at each encounter there are destroyed p_{rs} individuals (p_{rs} will evidently be a fraction) of one of the two species, for example of the species r, then in the unit of time $m_{rs} p_{rs} N_r N_s$ individuals of this species will be destroyed. Let us see how the influence that this has on the number of individuals of the other species can be calculated.

A rough calculation can be made in this way: Let us denote by $\beta_1, \beta_2, \ldots, \beta_n$ the average weights of all the individuals of the n species and by $P_1, P_2, \ldots, P_n$ the total weights of all the individuals belonging to each species. To get the number of individuals of each species it will suffice to take

$$N_1 = \frac{P_1}{\beta_1}, \ldots\ldots\ldots, N_r = \frac{P_r}{\beta_r}, \ldots\ldots\ldots, N_n = \frac{P_n}{\beta_n}.$$

Now if an individual of the species r is eaten by individuals of the species s the weight P_r will become $P_r - \beta_r$ while the weight P_s will become $P_s + \beta_r$ and for this reason the respective numbers of individuals of the two species will become roughly

$$\frac{P_r - \beta_r}{\beta_r} = N_r - 1, \qquad \frac{P_s + \beta_r}{\beta_s} = N_s + \frac{\beta_r}{\beta_s}.$$

Then in a very rough way we can say that in the unit of time, by virtue of the encounters of individuals of the species r with individuals of the species s, the diminution of individuals of species r will be given by

$$m_{rs} p_{rs} N_r N_s$$

and the increase of individuals of species s, also in the unit of time, will be given by

$$m_{rs} p_{rs} N_r N_s \frac{\beta_r}{\beta_s}.$$

Letting $m_{rs} p_{rs} \beta_r = a_{rs}$ the diminution of individuals of the species r will be

$$\frac{1}{\beta_r} a_{rs} N_r N_s$$

and the increase of individuals of the species s will be

$$\frac{1}{\beta_s} a_{rs} N_r N_s$$

or also letting $a_{rs} = -a_{sr}$ (supposing a_{sr} to be negative) we can say that in the unit of time, by virtue of their encounters, the numbers of individuals of the species r and of the species s increase respectively by

$$\frac{1}{\beta_r} a_{sr} N_r N_s, \qquad \frac{1}{\beta_s} a_{rs} N_r N_s,$$

and hence in the time dt, through their encounters, they increase respectively by

$$\frac{1}{\beta_r} a_{sr} N_r N_s \, dt, \qquad \frac{1}{\beta_s} a_{rs} N_r N_s \, dt.$$

The same can be said of each other pair of species. In other words the numbers $\frac{1}{\beta_1}, \frac{1}{\beta_2}, \ldots\ldots, \frac{1}{\beta_n}$ have been assumed as the equivalents of the individuals of the various species. In fact to grant that $\frac{1}{\beta_r}$ individuals of the species r can be transformed into $\frac{1}{\beta_s}$ individuals of the species s means that $\frac{1}{\beta_r}$ individuals of the species r are equivalent to $\frac{1}{\beta_s}$ individuals of the species s. Thus, taken in a very rough first approximation, we have as equivalent the reciprocals of the average weights, but it will suffice for us to take as hypothesis the existence of equivalent numbers, even if these do not coincide with the reciprocals of the average weights, in order to obtain the same results which we have now secured.

2. Let us call ε_r the coefficient of increase of the species r while that is alone, then if all the n species live together we shall have for the increase of the individuals N_r in the time dt

$$dN_r = \varepsilon_r N_r\, dt + \frac{1}{\beta_r} \sum_1^n{}_s\, a_{sr} N_r N_s\, dt,$$

whence we shall have the differential equations:

$$\frac{dN_r}{dt} = \left(\varepsilon_r + \frac{1}{\beta_r} \sum_1^n{}_s\, a_{sr} N_s\right) N_r, \qquad (r = 1, 2, \ldots, n)$$

or likewise

$$[B] \qquad \beta_r \frac{dN_r}{dt} = \left(\varepsilon_r \beta_r + \sum_1^n{}_s\, a_{sr} N_s\right) N_r, \qquad (r = 1, 2, \ldots, n)$$

in which

$$a_{rs} = -a_{sr}, \qquad a_{rr} = 0, \qquad \beta_1, \beta_2, \ldots, \beta_n > 0.$$

In the case of two species only, one of which feeds upon the other, we have considered the equations (§ 3, N. 1)

$$\frac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 N_2) N_1, \qquad \frac{dN_2}{dt} = (-\varepsilon_2 + \gamma_2 N_1) N_2.$$

If we put

$$-\gamma_1 = \frac{a_{21}}{\beta_1} \qquad \gamma_2 = \frac{a_{12}}{\beta_2}$$

these equations assume the form [B], with the need only of writing ε_2 instead of $-\varepsilon_2$ and understanding that ε_2 is negative. We see therefore that in this case there is no need of a special hypothesis.

For an association of n species we must distinguish the case in which the number of the species is even from that in which the number is odd.

In the first case the following statement can be proved: If there exists a stationary state[1]), placing the species in any state whatever different from the stationary state, the number of individuals of each species will remain limited between two positive numbers.

3. We must now establish some definitions in order to enunciate certain propositions without ambiguity.

If $N(t)$ indicates the number of individuals of a species and always remains included between two positive numbers, the species will be said to have limited variation between positive numbers.

If $N(t)$ approaches zero this signifies that the species is exhausting itself or also that the variation consists in a depletion.

If $N(t)$ is limited between two positive numbers, $N(t)$ will be said to have fluctuations if for $t > t_0$ (for t_0 however large) N has maximum and minimum values.

The fluctuations will be said to be damped if the oscillation (the difference between the upper and the lower limit) of $N(t)$ for $t > t_0$ can be made as small as we please by sufficiently increasing t_0. In this case and in this case only the fluctuations permit that N approach a fixed and finite limit for $t = \infty$.

$N(t)$ will be said to vary asymptotically and to approach asymptotically the limit q, if $N(t)$ has no fluctuations and approaches the fixed and finite limit q for $t = \infty$.

The limits for $t = \infty$ of the averages of $N_1, N_2, \ldots, N_n$ in the time $t_0 t$, will be called the asymptotic averages.

4. For an association of an even number of species we now express the following general propositions, omitting the demonstrations:

I) If there exists a stationary state for the biological association, the numbers of individuals of each species are limited between positive numbers, fluctuations always existing which are not damped, and the asymptotic aver-

[1]) That is a system of positive values of $N_1, N_2, \ldots, N_n$ satisfying the equations

$$0 = \varepsilon_r \beta_r + \sum_1^n{}_s a_{sr} N_s \qquad (r = 1, 2, \ldots, n).$$

ages of the numbers of individuals of all the separate species are the values corresponding to the stationary state.

II) The deviations from the stationary state can be made as small as we please, provided the initial state is sufficiently near to the stationary state.

In other words:

The stationary state is always a stable state[1]).

III) The small fluctuations of n species living together can be obtained by means of the superposition of $\frac{n}{2}$ fluctuations not damped and each having a period of its own.

As in general the periods $T^{(h)}$ will be incommensurable with each other, so the resulting fluctuation will not be periodic. Let it be observed that the number of the periods $T^{(h)}$ is equal to half the number of the species living together, but let it be called to mind that the laws of fluctuation now obtained hold in the case in which the number of species living together is even.

To summarize, the three theorems which we have designated by I, II, III, can be considered as three general laws of variation of an even number of species living together.

We can also enunciate the proposition: in order that there may exist a stationary state and ensuing fluctuations, some of the coefficients ε_r of increase must be positive and others negative, that is to say:

If by themselves all the species increase or all decrease, neither a stationary state nor ensuing fluctuations can exist.

If the number of species is odd it is not possible that the number of individuals of each species should stay limited between two positive numbers.

To thoroughly understand the significance of this theorem it is necessary to consider it as a purely theoretical result. Let us observe in the meantime that if one of the species should tend toward depletion, the number of the species will tend to become even and we shall return to the case considered previously.

But if the number of individuals of one of the species should increase indefinitely, it can be recognized that equations [B] will no longer be valid. In fact we have supposed the ε_r constants, that is to say independent of

[1]) The stability here is thought of in the sense analogous to the stability of equilibrium in mechanics.

the number of individuals present, which can be allowed if this number does not exceed a certain limit, but beyond this it can not be true any longer, whence the equations will be modified, at least for the changed value which will have to be attributed to the constants ε_r, in order to arrest the increase of that species which would increase indefinitely.

§ 8. Extension of the three fundamental Laws on Fluctuations to the Case of Associations of any Number whatever of Species.

1. In § 3 three fundamental laws on the fluctuations of two species living together have been stated. What is the extension of these to the general case of n species?

In § 7 it has been stated that in the case of an even number of species, if the fundamental determinant (the determinant of the system of equations B) is different from zero and if there exists a stationary state of the species without depletion, the variations of the numbers of individuals of the several species are limited between positive numbers and some fluctuations always exist which are not damped. Thus is enunciated the extension of the first law relative to two species. Evidently with this extension the property of periodicity is lost while that of fluctuation remains.

2. Let us admit as verified the aforementioned hypotheses and let us begin with an observation with regard to the extension of the second law (that is to say that of the invariability of the averages of the number of individuals) which, lacking periodicity, can not specify the duration of the time in which the averages must be taken. But we know that, taking the averages for infinitely long durations of time, these approach the roots of the equations of equilibrium. Now these roots are independent of the initial conditions, whence the second law remains unaltered if we take as averages (cf. § 7) of the numbers of individuals of separate species, the limits of the same averages for infinitely long durations of time (asymptotic averages).

3. The question now is to see what form the third law will assume in general, namely the law of disturbance of the averages, always granting as verified the aforesaid hypotheses. For the averages of the numbers of individuals of the several species we shall always assume the asymptotic averages.

In the third law (§ 3, N. 8) a distinction is made between the species

that is eaten and the species feeding upon the other. When we pass to more than two species, it may be that the individuals of one species are eaten by those of another and themselves feed upon the individuals of a third species. Wishing to keep the distinction between species that are eaten and those feeding upon others it is necessary to admit that if a species A feeds upon another there is not any species that eats A and hence that if a species B is eaten by another, it does not feed upon any other species of the biological association.

4. Now we can state the theorem that if we keep the preceding hypotheses the numbers of the species eating others must be equal to the number of the species fed upon.

Whence we can suppose that $n = 2p$ and that the species $1, 2, \ldots, p$ are feeding upon others and the species $(p+1), (p+2), \ldots, 2p$ are fed upon. Then for the existence of a stationary state $\varepsilon_1, \varepsilon_2, \ldots, \varepsilon_p$ must be negative and $\varepsilon_{p+1}, \varepsilon_{p+2}, \ldots, \varepsilon_{2p}$ must be positive.

Now let us increase

$$|\varepsilon_1|, \qquad |\varepsilon_2|, \ldots\ldots, |\varepsilon_p|$$

and let us diminish

$$|\varepsilon_{p+1}|, \qquad |\varepsilon_{p+2}|, \ldots\ldots, |\varepsilon_{2p}|$$

namely let us destroy one set of species as much as the other in proportion to the number of individuals which they have respectively. Some one of the

$$N_{p+1}, N_{p+2}, \ldots\ldots\ldots, N_{2p}$$

satisfying the equations of equilibrium will have to increase and some one of the

$$N_1, N_2, \ldots\ldots\ldots, N_p$$

satisfying the same equations must diminish. Reciprocally if none of the $N_{p+1}, \ldots\ldots, N_{2p}$ decreases, but all or some increase, if none of the $N_1, \ldots\ldots, N_p$ increases, but all or some diminish, then $|\varepsilon_{p+1}|$, $|\varepsilon_{p+2}|, \ldots\ldots, |\varepsilon_{2p}|$ must diminish and $|\varepsilon_1|, |\varepsilon_2|, \ldots\ldots, |\varepsilon_p|$ must increase, that is to say individuals of the species feeding upon others must be destroyed, as well as of the species eaten, in proportion to their number.

It is in this that the extension of the third law consists, which (recalling the significance of the roots of the equations of equilibrium) can be enunciated as follows:

In a conservative association of even order, with determinant different from zero, for which a stationary state exists and the species feeding upon others can be distinguished from those eaten, if all the species are destroyed uniformly and in proportion to the number of their individuals, the asymptotic averages of the number of individuals of some of the species eaten (if not of all) will increase, and the asymptotic averages of the numbers of individuals of some of the species feeding upon others (if not of all) will diminish.

Naturally this proposition holds up to a certain limit of destruction (cf. §§ 4, 5), and if the roots of the equations of equilibrium are positive.

§ 9. Case in which the Coefficient of increase of each separate Species depends on the Number of Individuals of that same Species.

1. Various times in preceding sections we have had occasion to consider cases in which the calculation would lead to an indefinite increase of the number of individuals of one or more species. Such a result must be considered theoretical and we have not failed to give explicit warning on this as in N. 1 of § 4, observing that with the increase of the number of individuals the equations must become invalid, and in particular that the coefficients of increase must be modified because of the indefinite increase in the number of individuals.

This necessitates a consideration of the influence which the number of individuals of one species has upon its coefficient of increase. It is evident that this effect can be neglected as long as the number of individuals does not exceed certain limits, but it is necessary to take it into account when the calculation leads to an infinite increase of individuals. Let us see how this can be done.

In the case in which only one species exists, and if we admit the coefficient of increase as constant and equal to ε, we shall have

$$\frac{dN}{dt} = \varepsilon N$$

where N denotes the number of individuals, whence

$$N = N_0 e^{\varepsilon t}$$

where N_0 is the initial number of individuals. If ε is positive N will increase indefinitely.

Now let us suppose that the coefficient of increase is not constant, but is given by $\varepsilon - \lambda N$ where ε and λ are positive constants. We shall have

$$N = \frac{C\varepsilon e^{\varepsilon t}}{1 + C\lambda e^{\varepsilon t}}$$

and hence

$$\lim_{t=\infty} N = \frac{\varepsilon}{\lambda}.$$

Corresponding changes can be made in equations $[B]$, and from a study of them we may state the theorem:

If a stationary state exists and if the coefficients of increase of one or more species decrease linearly with the increase of the number of the respective individuals, while the coefficients of increase of the other species are constants, starting out from any initial state whatever different from the stationary state, we shall have for the first species either asymptotic variations or fluctuations which will be damped. If all the coefficients decrease in the aforesaid manner the system will tend toward the stationary state[1]).

In certain ways the actions which tend to damp the increase of each species with the increase of the number of individuals belonging to it produce an effect analogous to that of internal attritions in a material system, that is they damp the fluctuations.

§ 10. Conservative and dissipative Biological Associations.

1. The considerations of the last section can be notably extended; we shall thus be led to a fundamental classification of biological associations.

To this end let us suppose that the coefficients of increase depend linearly in any way upon the number of individuals, not only of each species, but of the various species and let the effects of the encounters of individuals of different species be felt in any way whatever, but constant, by the species themselves, proportional to the number of encounters, without further concern over the satisfaction of the hypothesis of § 7, N. 1.

[1]) Also if some coefficients λ_r are zero, the state of the system can approach the stationary state. (Cf. § 8, N. 4.)

It is easy to be convinced with particular examples that according to different cases there may be asymptotic variation and damped fluctuations.

Equations [B] then assume the general form

$$[C] \qquad \frac{dN_r}{dt} = \left(\varepsilon_r - \sum_1^n{}_s\, p_{rs} N_s\right) N_r$$

where the coefficients ε_r and p_{rs} are any constants whatever.

We can consider the ε_r as dependent on the constant causes of increase or decrease of the species, and the other terms as dependent upon the reciprocal actions of the individuals. Evidently with this there is shown an extension of the concept of reciprocal action among the various individuals much greater than has been done previously.

If each species were alone the ε_r would be their coefficients of increase, while

$$\varepsilon_r - \sum_1^n{}_s\, p_{rs} N_s$$

are the coefficients of increase of the same species as a result of their living together. We shall call these last the true coefficients of increase and ε_r the rough coefficients of increase or also we shall call them simply coefficients of increase when confusion can not arise between the two sets.

2. First of all we can say that it is sufficient that one of the coefficients be positive, in order that all the species should not be exhausted.

Let the quantities $\alpha_1, \alpha_2, \ldots, \alpha_n$ be positive and let us place

$$F(N_1, N_2, \ldots\ldots, N_n) = \sum_1^n{}_r \sum_1^n{}_s\, \alpha_r p_{rs} N_s N_r .$$

We shall have the theorem:

If the form F is positive definite, there will exist a number N such that none of the numbers $N_1, N_2, \ldots, N_n$ can remain larger than N, starting from a certain instant.

In fact from [C] it follows that

$$\sum_1^n{}_r\, \alpha_r \frac{dN_r}{dt} = \sum_1^n{}_r\, \alpha_r \varepsilon_r N_r - F(N_1, N_2, \ldots\ldots, N_n).$$

Letting $N_r = 1$, let us denote by m_r the lower limit of the values of F for all possible values of $N_1, N_2, \ldots, N_{r-1}, N_{r+1}, \ldots, N_n$. m_r will be > 0. Let m be the smallest of the numbers $m_1, m_2, \ldots, m_n$. Besides let

$$\sum_1^n{}_r \left| \alpha_r \varepsilon_r \right| < E .$$

Let us suppose that N_r after a certain instant t_1 stays greater than

$$\frac{E+1}{m} = N .$$

Let us denote by $M(t_2)$ the greatest of the numbers $N_1(t_2)$, $N_2(t_2)$, ..., $N_n(t_2)$ where $t_2 > t_1$.

Then we shall have

$$F(N_1, N_2, \ldots\ldots, N_n)_{t=t_2} > mM^2(t_2)$$

$$\sum_1^n{}_r \alpha_r \varepsilon_r N_r(t_2) < EM(t_2)$$

whence it follows that

$$\left(\sum_1^n{}_r \alpha_r \frac{dN_r}{dt} \right)_{t=t_2} > (E - mM(t_2))\, M(t_2) .$$

Now

$$M(t_2) > \frac{E+1}{m}$$

hence

$$\left(\sum_1^n{}_r \alpha_r \frac{dN_r}{dt} \right)_{t=t_2} < -\frac{E+1}{m}, \qquad (t_2 > t_1),$$

a consequence of which would be that starting from a certain moment, some one of $N_1, N_2, \ldots, N_n$ would have to become negative which is absurd, since N_r can be only positive as follows also from [C]. In fact from these equations is derived

$$N_r = N_r^0 e^{\int_0^t (\varepsilon_r - \Sigma_s \Gamma_{rs} N_s)\, dt}$$

where N_r^0 is the value of N_r for $t = 0$, whence as N_r^0 is positive so will N_r remain. Therefore there exists the number $N = \frac{E+1}{m}$ such that each N_r after a certain instant t_1 can not remain greater than that number.

Combining the last two theorems now we can state the proposition: If at least one of the coefficients of increase is positive and

if the form E is positive definite the biological association will be stable.

The stability consists in the fact that the whole association does not tend toward depletion, and no one species can increase indefinitely.

As the N_i are all positive so the preceding theorem can be extended to the case in which the form F is not zero except when every $N_i = 0$ and is positive for all positive values of the N_i.

3. We can easily see that if the form F is positive definite the determinant formed with the p_{rs} can not be zero. Let us suppose that it is zero. Then there would exist some numbers $N_1, N_2, \ldots, N_n$ (positive, negative, or zero, but not all zero) which would satisfy the equation

$$\sum_1^n{}_s p_{rs} N_s = 0$$

and hence

$$0 = \sum_1^n{}_r \sum_1^n{}_s \alpha_r p_{rs} N_s N_r = F(N_1, N_2, \ldots, N_n)$$

which contradicts the hypothesis that the form F is positive definite.

Having made this premise, let us suppose that the equations

$$[C'] \qquad \varepsilon_r - \sum_1^n{}_s p_{rs} N_s = 0$$

when solved with respect to N_s give the solutions $q_s \neq 0$. We shall have then the identities

$$\varepsilon_r = \sum_1^n{}_s p_{rs} q_s$$

whence equations $[C]$ will become

$$\frac{dN_r}{dt} = -\sum_1^n{}_s p_{rs}(N_s - q_s) N_r$$

that is by letting

$$\frac{N_r}{q_r} = n_r$$

we shall have

$$[24] \qquad \frac{dn_r}{dt} = -\sum_1^n{}_s p_{rs} q_s (n_s - 1) n_r .$$

From these equations it follows that

$$\frac{1}{n_r}\frac{dn_r}{dt} = -\sum_1^n{}_s p_{rs} q_s (n_s - 1).$$

Let α_r represent positive constant quantities; then we shall have

$$\sum_r \alpha_r q_r \frac{n_r - 1}{n_r}\frac{dn_r}{dt} = -\sum_1^n{}_r \sum_1^n{}_s p_{rs}\, \alpha_r\, q_r\, q_s (n_s - 1)(n_r - 1).$$

Let us place

[25] $$\frac{1}{2}(p_{rs}\alpha_r + p_{sr}\alpha_s) = m_{rs} = m_{sr},$$

[26] $$F(x_1, x_2, \ldots, x_n) = -\sum_r \sum_s m_{rs} x_r x_s,$$

then the preceding equation can be written

$$\frac{d}{dt}\sum_r \alpha_r q_r (n_r - \log n_r) = -F(x_1, x_2, \ldots, x_n)$$

where

$$x_r = (n_r - 1) q_r.$$

Integrating and passing from logarithms to numbers, we shall have

$$\left(\frac{e^{n_1}}{n_1}\right)^{\alpha_1 q_1}\left(\frac{e^{n_2}}{n_2}\right)^{\alpha_2 q_2}\ldots\ldots\left(\frac{e^{n_n}}{n_n}\right)^{\alpha_n q_n} = Ce^{-\int_0^t F dt}$$

where C is a positive constant.

If $q_1, q_2, \ldots, q_n$ are positive, namely if there exists a stationary state and if $\alpha_1, \alpha_2, \ldots, \alpha_n$ can be so chosen that the quadratic form [26][1]) is identically zero, the numbers of individuals of the separate species will be limited between positive numbers and fluctuations must exist which are not damped. If a stationary state exists and if the positive constants $\alpha_1, \alpha_2, \ldots, \alpha_n$ can take such values as to make the form [26] positive we can say that the variation of the numbers of individuals of the separate species is confined between two positive numbers[2]); but if the form is

[1]) In this case, in order that the determinant of the p_{rs} be different from zero, n will have to be even.

[2]) This property leads at once to the recognition that the limits of the averages of $N_1, N_2, \ldots, N_n$ in intervals of time increasing infinitely are $q_1, q_2, \ldots, q_n$.

positive definite besides this it will follow that all the variations of the separate species will be asymptotic or there will be damped fluctuations which make the biological association tend toward the stationary state.

The proof of this proposition is analogous to the proof of the proposition of § 9.

Besides we find that every time the form [26] is positive the limits of the average of $N_1, N_2, \ldots, N_n$ in intervals of time increasing indefinitely will be $q_1, q_2, \ldots, q_n$.

The expression F can be written

$$[27] \qquad F = \sum_1^n{}_r \sum_1^n{}_s \alpha_r p_{rs} (N_r - q_r)(N_s - q_s).$$

In § 9 the action damping the fluctuations has been compared to an internal attrition. The preceding form F can be taken as a measure of this damping action, which characterizes the tendency toward the stationary state of the group of all the species, and in fact, if F is zero the biological association will not tend toward a limit state, while if it is positive definite the association will tend toward the stationary state.

We shall call the form $F(x_1, x_2, \ldots, x_n)$ the fundamental form and the equations $[C']$ the equations of equilibrium. We exclude the case in which these equations have zero roots, that is we exclude the possibility that the stationary state can coincide with the exhaustion of any one of the species.

4. Now we can review the hypothesis of § 7, N. 1, and get a deeper insight into its significance.

Let us suppose we give to each individual of the species r a positive value α_r. The value of the whole biological association will be $V = \sum_1^n{}_r \alpha_r N_r$ whence, from the equations $[C]$ will follow

$$dV = \sum_1^n{}_r \alpha_r \varepsilon_r N_r dt - \sum_1^n{}_r \sum_1^n{}_s p_{rs} \alpha_r N_r N_s dt.$$

The increase of value of the biological association in the time dt consists then of two parts

$$dV_1 = \sum_1^n \alpha_r \varepsilon_r N_r dt$$

$$dV_2 = \sum_1^n{}_r \sum_1^n{}_s p_{rs} \alpha_r N_r N_s dt.$$

The first is due to the constant causes of increase and decrease of each species (particularized by ε_r), and the second is due to the reciprocal actions of the various individuals in the general sense understood before.

If the α_r can be chosen in such a way that dV_2 be zero whatever may be $N_1, N_2, \ldots, N_n$, the value of the biological association will not change in consequence of the reciprocal actions of the individuals. A biological association of this nature, namely in which it is possible to assign to the separate individuals such values that their reciprocal actions keep the value of the entire association constant will be said to be conservative. Evidently for a conservative system the hypothesis of § 7, N. 1 is satisfied. Reciprocally, if that hypothesis is holding and the reciprocal actions between individuals of the same species are negligible, the biological association will be conservative.

Absolutely conservative biological associations are probably ideals which can only approximate the conditions effective in nature. But a special example of conservative systems is considered in § 7, N. 2.

When to separate individuals there can be assigned values (equal for those of the same species) such that the fundamental form F be positive definite the reciprocal actions between individuals will tend to diminish the value of the entire association which can therefore be called dissipative. It seems that in many real cases biological associations must approximate dissipative associations.

§ 11. General Theorems on conservative and dissipative Biological Associations.

1. A proposition can be stated which says the value of a conservative biological association: 1) approaches zero if all the coefficients of increase are negative and only when all are negative; 2) approaches infinity if all are positive[1]).

The first part of this proposition can be extended to dissipative systems.

In fact from [C], using [25], it follows that

$$\sum_1^n{}_r \alpha_r \frac{dN_r}{dt} = \sum_1^n{}_r \alpha_r \varepsilon_r N_r - \sum_1^n{}_r \sum_1^n{}_s m_{rs} N_r N_s .$$

[1]) In this statement we have excluded the case of zero coefficients of increase as we shall also exclude it in the extension of the proposition.

If the form

$$\sum_1^r \sum_1^s m_{rs} N_r N_s$$

is positive definite or semi positive definite then

$$\sum_1^n \alpha_r \frac{dN}{dt} < \sum_1^n \alpha_r \varepsilon_r N_r$$

and if

$$\varepsilon_r < -\varepsilon, \qquad (r = 1, 2, \ldots\ldots, n)$$

ε being a positive quantity, we shall have

$$\sum_1^n \alpha_r N_r < \sum_1^n \alpha_r N_r^o e^{-\varepsilon t}$$

which proves that the value of the biological association approaches zero if all the coefficients of increase are negative; then in order that the biological association should not exhaust itself it is sufficient that one only of these coefficients should be positive (cf. § 10 N. 2).

As for the second part of the preceding proposition, by virtue of what is shown in § 10, N. 2 it must be replaced by: the value of a dissipative biological association stays limited.

For a conservative association it is possible to prove the following theorem: None of the several species can either exhaust itself or increase indefinitely in a finite time.

2. Let us pass to the case of dissipative associations: For these we know that the number of individuals of each species is limited, but it can be proved that the number can not however become zero in a finite time.

The conclusion will be: In a dissipative association no species can exhaust itself in a finite time, whereas the number of individuals of each species is limited.

3. Then we can state the theorem: In order that in a dissipative association or in a conservative association of even order (with determinant different from zero) the number of individuals of each species should remain between positive numbers, a necessary and sufficient condition is that the roots of the equations of equilibrium be positive.

§ 12. Fluctuations Peculiar to the System, forced Fluctuations, and the Principle of their Superposition.

1. In equations [*C*] of § 10, which can be considered as the most general and as summing up all those preceding, we have supposed that the coefficients of increase ε_r be constants; but really these change and in general their changes are periodic or due to the addition of more periodic terms. Certainly in all practical cases we shall have to consider an annual period in connection with the changes of seasons and meteorological conditions. But nothing precludes the existence of other periods.

Let us try to take account of these periodic disturbances of the coefficients of increase, for which let us substitute

$$\varepsilon_r + g'_r \cos kt + g''_r \sin kt$$

for ϵ_r where g'_r, g''_r and k are constant quantities.

Equations [*C*] will become

[D] $$\frac{dN_r}{dt} = (\varepsilon_r + g'_r \cos kt + g''_r \sin kt - \sum_1^n{}_s p_{rs} N_s) N_r$$

and [24]

$$\frac{dn_r}{dt} = (g'_r \cos kt + g''_r \sin kt - \sum_1^n{}_s p_{rs} q_s (n_s - 1)) n_r$$

in which we shall suppose each q_s positive.

Let us observe that ε_r are the average values of the coefficients of increase during the period $\frac{2r}{k}$; we can then state the theorem: If the coefficients of increase are periodic and their average values differ little from the changeable values, and if taking these average values as the coefficients of increase, there result asymptotic variations or damped fluctuations or fluctuations not damped near to a stationary state (variations peculiar to the system), then for small fluctuations corresponding to periodic coefficients of increase the principle of superposing on the forced fluctuations the variations peculiar to the system will be applicable, that is to say small fluctuations will be obtained, superposing on the variations peculiar to the system those which are forced having the period of the coefficients of increase, when that period does not coincide with any of the periods of the casual fluctuations peculiar to the system.

§ 13. Disturbance Produced in a Biological Association having a stationary State by the Addition of a new Species.

1. By using results of preceding sections we can state the following theorem: If a stationary state exists for a certain biological association, but by adding a new species to it the possibility of the stationary state is lost because the equations of equilibrium have a negative root for the number of individuals of the species added, the small variations of the whole association (supposed dissipative) will consist of a variation of the original association near to its stationary state superimposed on a depletion of the new species[1]).

For this reason the species added will tend to a depletion and the others will approach a variation near to the stationary state, whence the addition of the new species will produce a disturbance which will tend to disappear.

§ 14. Study of a particular Biological Association of three Species.

1. As an example of the treatment developed previously let us examine a particular case which, because of the theory shown above, can be treated mathematically in full.

Let us suppose three species living together in a limited environment, for example on an island. Of these three species let the first eat the second and this the third and not vice versa. For example we can take a species of carnivorous animals that feed upon an herbivorous species and this in turn feeds upon a vegetable species, admitting that for this last the same treatment holds as that used for the animals. Another example is furnished by plants their parasites and parasites of these parasites.

2. Let us admit the biological association to be conservative (cf. § 10).

If we indicate the number of individuals of the three species by N_1, N_2, N_3 we shall have equations (see [B], § 7, N. 2)

$$\beta_1 \frac{dN_1}{dt} = (\beta_1 \varepsilon_1 + a_{21} N_2 + a_{31} N_3) N_1$$

$$\beta_2 \frac{dN_2}{dt} = (\beta_2 \varepsilon_2 + a_{12} N_1 + a_{32} N_3) N_2$$

[1]) It is opportune to compare this theorem with that of § 11.

$$\beta_3 \frac{dN_3}{dt} = (\beta_3 \varepsilon_3 + a_{13} N_1 + a_{23} N_2) N_3$$

where β_1, β_2, β_3 are constant quantities.

In our case we must take

$$\varepsilon_1 = -l < 0, \qquad a_{21} = a > 0, \qquad a_{31} = 0,$$
$$\varepsilon_2 = -m < 0, \qquad a_{12} = -a < 0, \qquad a_{32} = b > 0,$$
$$\varepsilon_3 = k > 0, \qquad a_{13} = 0, \qquad a_{23} = -b < 0,$$

where a, b, l, m, k are constant quantities.

According to values of these coefficients of increase and of voracity and values of β_1, β_2, β_3, the following cases and subcases can be presented:

1st Case.— $\beta_3 ka - \beta_1 lb < 0$

The food furnished to the carnivori by the herbivori is not sufficient to maintain the carnivorous species and this is depleted, while the herbivori and the plants tend toward a periodic fluctuation not damped. (We can suppose the coefficient of increase of the plants, k, to be constant because in this case the vegetable species can not increase indefinitely.)

2nd Case.— $\beta_3 ka - \beta_1 lb > 0$

If the coefficient of increase of the vegetable species were constant, the number of individuals in it would grow indefinitely, hence it is proper to suppose that this coefficient decreases proportionally to the number of individuals.

2nd Case, subcase a). — The food provided by the plants is not sufficient to maintain the herbivori, hence the herbivorous species and the carnivorous species die out, while the vegetable species tends toward a constant value.

2nd Case, subcase b). — The plants are sufficient to maintain the herbivori, but there is not sufficient food for the carnivori through the herbivori, hence the carnivorous species is depleted, while the herbivori and plants tend toward a damped fluctuation, and finally to a stationary state.

2nd Case, subcase c). — The food is sufficient so that all the species live, and through asymptotic and damped variations they all tend toward a stationary state.

On Sex and Growth Investigations on the Freshwater Eel in Dutch Waters.

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Section I. Numerical relations of the sexes.

Since Syrski (19) in 1874 made known the sexual organs of the male freshwater eel, countless sex determinations of eels have been made, and these soon revealed the remarkable fact that as a rule males are to be found in estuaries and near mouths of rivers, whereas females generally live in the upper reaches of rivers, in brooks, ponds etc., in short in all kinds of water really fresh.

This has been stated so often that only a few remarks are needed to elucidate this governing rule in the distribution of the sexes. Investigations have been carried on for years on this subject in this country, care being taken to choose only the small eels, at least under 42 cm. length, larger specimens turning out, almost without exception, to be females; males of more than 42 cm. are, in Holland at least, exceedingly rare.

The localities from which the numerous samples were taken are to be gleaned from the chart here given (see p. 53); we may unite them into the following districts:—

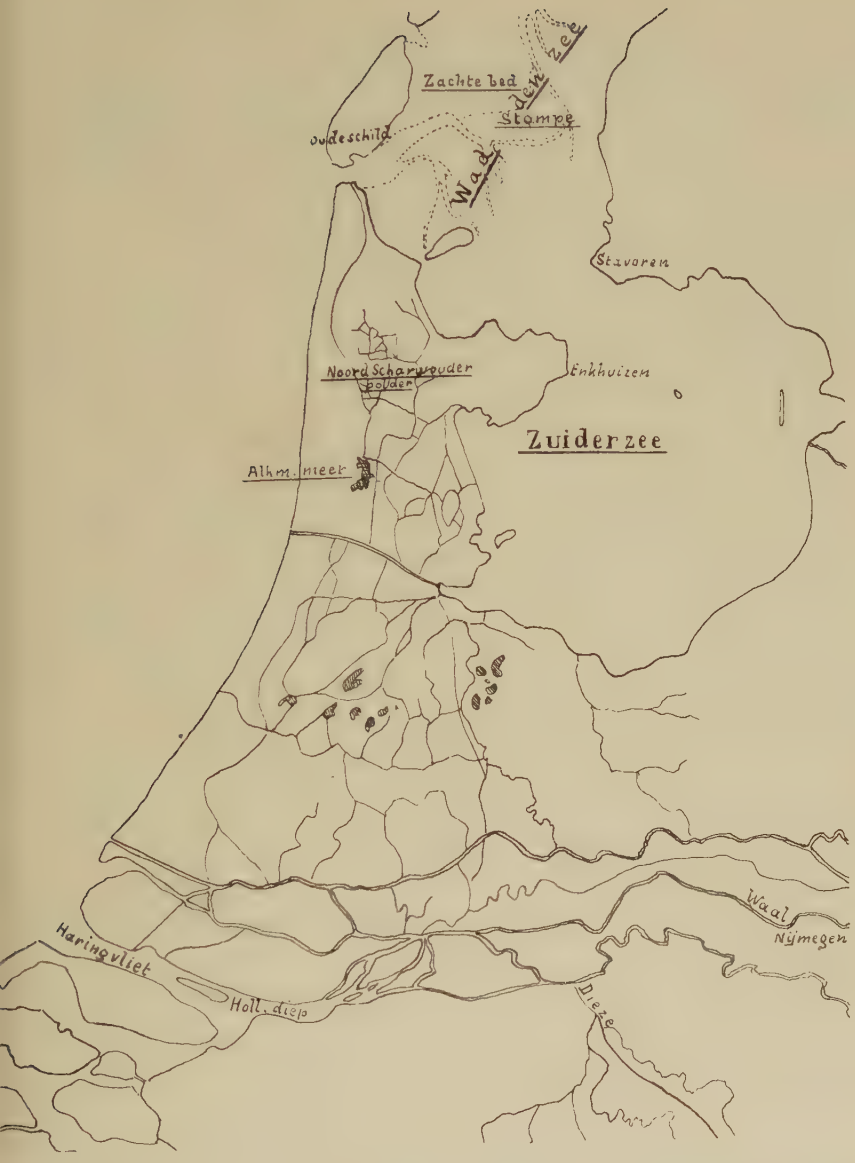
I) Interior of Zuiderzee bound northwards by a line between Enkhuizen and Stavoren;

II) Waddenzee, northwards of the said line and confined outwards by the belt of islands near the coast;

III) Haringvliet and Hollandsch Diep, extending between the islands of Ysselmonde, Putten and Voorne on the north side, and the islands of Overflakkee and Goeree to the south;

IV) Waal near Nymegen, as example of upper reach of river;

V) Inland waters in North Holland and in other provinces.



A glance at Table 1 in which the results of thousands of sex determinations in different months and during a period of five years are summarised reveals at once the enormous numerical preponderance of males in the Zuiderzee proper. We are indeed justified in stating that among the small eels from this water (which are largely transplanted into inland waters) females are practically absent. Choosing an arbitrary division at a length of 27 cm. it may be said that, in a total of 1724 individuals examined, only 24 females (1.4 per cent.) could be detected.

Table I. Numerical relation of sexes in various Dutch districts in eels of 42 cm length and under.

District	Numb. exam.	Percent		Percent at lenghts up to 27 cm (incl.)		Percent at lengths from 28—42 cm (both incl.)	
		♂	♀	♂	♀	♂	♀
I. (Zuiderzee)	2584	94	6	98.6	1.4	85.1	14.9
II. (Waddenzee)	775	70	30	77.7	22.3	58.5	41.5
III. (Haringvliet, Holl.diep)	1001	87	13	94.6	5.4	56.9	43.1
IV. (Waal)	246	76	24	82.0	18.0	48.0	52.0
V. (Inland waters)	182	..	..	..	..	28.0	72.0

Remarkable is the much larger proportion of females in the Waddenzee, most striking even in the smaller specimens of at most 27 cm. length; this is a fact which we are not able to explain. Marcus (14) examined a number of eels caught on the East Frisian coast and found in a total of 153 specimens (ranging as in my series, which contained 462 specimens, from 19 to 27 cm.) a percentage for the females of 17 per cent. — less than on the Dutch coast, but worth noting, as the mouth of the Elbe yielded only 10 per cent. females out of a total of 550 specimens between the said lengths.

Among eels caught up river (Waal near Nymegen) the females increase largely in number; from 28 cm. onwards they even outnumber the males; but below this length they are even here, in perfectly fresh water, in the minority (18 per cent.).

All the facts here collected tend to confirm the general rule of the local separation of sexes in the eel, at least in broad outline. But it has long since attracted attention that everywhere the female sex becomes much more numerously represented in the larger specimens, whereas they seem to be rare, if at all present, in the smaller eels. This phenomenon can only partly be accounted for by the fact that the growth of females is more rapid than that of males, so that the former sex passes through the successive lengths within a shorter lapse of time. A most careful search in the haunts of female eels yields a number of small specimens which only exceptionally turn out to belong to this sex; the majority of these small ones seem to be males, according to their tough string-like sexual organs, which in some cases even show the characteristic fringe of lobes peculiar to the gonads of the male sex. But are they really "males"?

We now come to Grassi's presumption (7) apparently confirmed by other authors, as Mazza (15.16) and d'Ancona (1.2), that small eels,

as a rule, even to a length of 30 cm. in some cases, are not yet sexually defined, though possessing a truly lobed "testis", but are capable of developing, presumably according to outer circumstances, these organs into real ovaries. Histological investigation shows in this undefined organ large cells, "oocytes", which, if the individual eel becomes a female, multiply and enlarge, till finally a typical ovary has been formed.

There is no need to devote much space to GRASSI's investigations, careful and interesting though these may be, which have caused much attention, not only in Italy where several of his pupils have continued his work, but also in Germany [see reviews by A. WULFF (21.22), WITSCHI (20) and EHRENBAUM (5)]. The last named author, justly considered one of the chief authorities on the biology of the eel, is now apparently convinced of the truth underlying GRASSI's assertions. Only a real experiment is able to verify this.

Such an experiment has been carried out by me by putting a sample of young eels (about 80 sp.) in a tank of concrete, filled with running freshwater, in the aquarium-building of the Amsterdam Zoological Garden in September 1922. These eels were caught in baskets ("kubben") near Pampus in the south west corner of the Zuiderzee, a locality where according to previous researches males are so prevalent among the small eels that practically no females occur. Part of this sample was examined directly after the catch, and all of them turned out to be males; the rest, ranging in length from 20–25 cm., were put into the tank, where they fed upon dead shrimps. After one year, in November 1923 21 sp. were examined and the sexual organs showed no sign of changing; they all, as a matter of fact, showed the characteristic lobe-like appearance, peculiar to the Syrski gonads. Two years afterwards in the autumn of 1925 the remaining ones which at that time had grown to a length of 30—45 cm. were dissected, and then the remarkable fact was discovered that all of them, 12 sp. in all, were certainly females, with true ovaries in which numerous ova were developing.

This result, we may say, is almost too conclusive, and similar experiments on an enlarged scale and under varied circumstances are to be carried out. It will be especially interesting to state in what numerical proportion glass eels will develop according to external conditions either into males or into females, as the case may be (distinguishing between the various average length-groups of the fry if any such differences do exist) and to continue BELLINI's experiments (3) which caused so much controversy[1]). It will likewise be necessary to repeat MAZZA's experiments

[1]) JOHS. SCHMIDT (18), HEIN (10) and LÜBBERT (13) tested the truth of BELLINI's statements about three length-groups in ascending glass eels, but they could find

(15.16) which showed that even undoubted small silver eels if kept five years in a freshwater tank could change completely into females as was proved by their possessing true ovaries.

If we were able to influence the future sex in small eels by transplanting them from one water to another, this would be a fact of great importance. Nevertheless it should be borne in mind that also in freshwater males do normally occur. In the beginning of October 1920 I investigated a sample of (mostly) silver eels caught with eel set nets ("fuiken") in the Dieze near 's-Hertogenbosch (see chart). Though only the smaller specimens (length between 27—41 cm.) were examined I found no less than 97 males and only 4 undoubted females. A small sample from the "Alkmaarder Meer" near Alkmaar (length ranging from 23—32 cm.) proved to contain 32 males and 10 females.

Experience of those who transplanted small eels of about 25 cm. length from the Zuiderzee to the inland waters of North Holland seems on the other hand, so far as the results are to be trusted, to confirm the surmise that these very eels in the course of a few years yield a large percentage of females, notwithstanding the fact that they are, at the time of transplanting apparently "males".

Section II. Age Determinations.

Gemzöe (6) nearly twenty years ago first described the method of age assessment of eels by means of the scales, and since then this method has been applied by a series of authors among whom we may name Wundsch (23), Haempel and Neresheimer (9), Nordqvist and Alm (8) and quite recently Jespersen (12). German investigators [Ehrenbaum and Marukawa (4)] afterwards recommended the otolith method and their practice has been adopted by Marcus (14) and Hornyold (11).

There can be no question that with small eels, in which the otoliths have not yet become too opaque, these are to be preferred, though their extraction, their handling and — last not least — their reading involve much work and a great deal of uncertainty in many cases. In examining thousands of eel otoliths, after grinding and putting them in xylol, I only exceptionally found them to be so clear that no difference of opinion could possibly arise about the exact number of growth rings.

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no proof of their existence after measuring a great many of these eels from the Severn. Afterwards Grassi (7) and d'Ancona (1, 2) experimented with the larger length-groups of glass eels (above 75 mm.) which, according to Bellini's results, should develop mostly into females, the eels, however, after having been reared for four years turned out to be males, for at least 24.4 per cent.

As I was chiefly concerned, however, with small eels, up to about 42 cm. length, I considered the otoliths more valuable than the scales, for the latter, though of course much easier and more readily to be got, present the great disadvantage that they do not appear at a fixed age of the individual eel but at a certain length of about 16—18 cm., which length is generally attained in the III-group (fourth year after metamorphosis), but in many cases in the II- or even in the IV-group[1]). The use of scales can therefore only afford a relative value, but it is the only method applicable when large eels, in which the thick otoliths are generally useless, are dealt with. The best thing is to rely on both methods, and I have done so in a number of samples, but this proceeding takes really a lot of time.

Another difficulty, on which especially MARCUS (14) is emphatic, lies in the circumstance that both scales and otoliths add a new growth zone relatively late in the warmer season, especially so in the case of otoliths. A new year-ring in the scales does not appear before June, in the otoliths not even before September, and this first appearance varies according to locality in which the eels have been caught. As eels are taken in this country nearly exclusively in the summer months there is only one way to avoid mistakes: to count only such growth-zones as are distinctly complete, so that we take the age of the eel in full years. This way of dealing with the material has been recommended and used by MARCUS and I have followed his advice throughout my work.

We may now consider the growth of eels in the various districts enumerated in chapter I.

A. Zuiderzee.

The following table (T. II, p. 59) shows the growth-rate of eels (mostly males or, as we now know, as yet of undefined sex) in the interior (southern) part of the Zuiderzee; the age is given in full years. "Four years" f.i. therefore means, that four years have elapsed since metamorphosis in the life of the particular eel which is now in the course of the fifth year.

In all, more than 850 specimens were examined. Samples were taken during the summer months of 1920, 1921 and 1922 and the data are here put in a concise form, regardless of year of catch, locality where caught in the Zuiderzee and fishing gear used. The growth is shown in Fig. 1.

In comparing the age determinations by EHRENBAUM and MARU-

[1]) This important fact was first discovered by EHRENBAUM and MARUKAWA and afterwards confirmed by MARCUS.

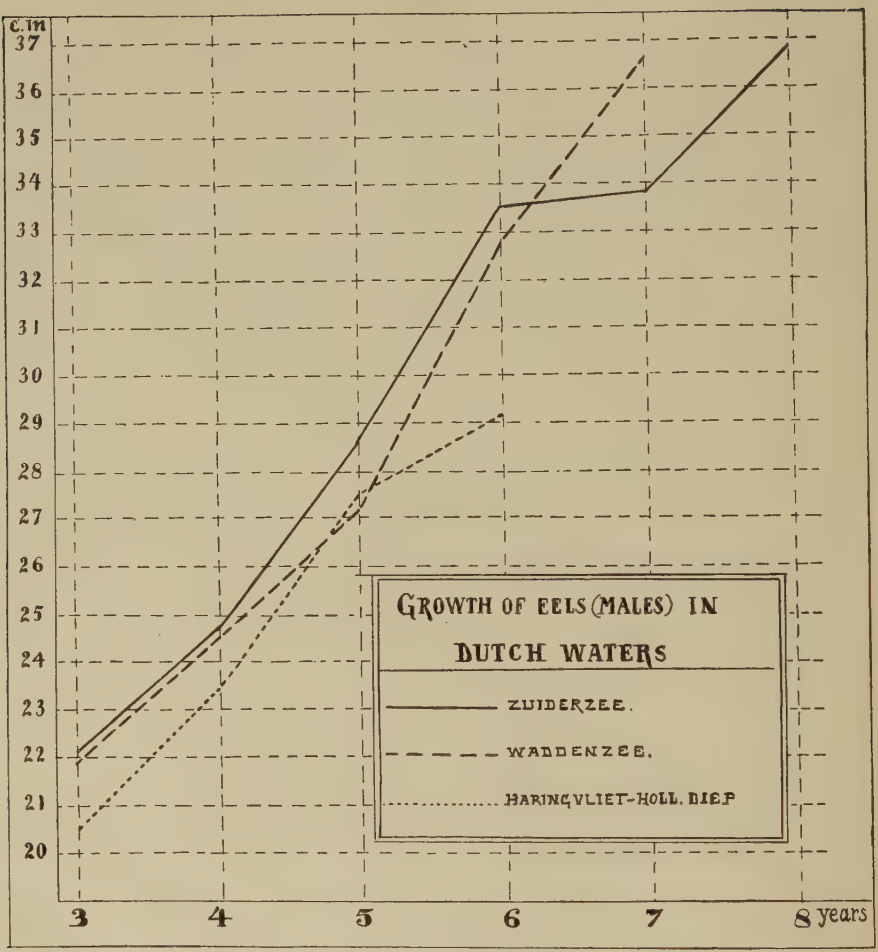

Fig. 1.

KAWA (4) with ours we are struck by the rather great difference in length between eels of equal age in the Zuiderzee and the mouth of the Elbe. But there is the important fact that the eels from the Elbe were examined in the course of late autumn and early winter: in a period in which the growth for the year is nearly completed, whereas my samples are mostly taken in full summer and autumn, when the growth is in full swing, and here the current period of growth is not taken into account. So we may say that broadly speaking "four years" of age in my age assessments means "five years" in the German tables, and so the difference above spoken of seems to be of no great importance.

Only for eels of three years of age is there a marked difference between

Table II. Average growth of eels in the Zuiderzee.
(Age given in completed years).
Figures between brackets indicating number of specimens examined.

Sex	Length in cm after					
	3 years	4 years	5 years	6 years	7 years	8 years
♂ or ♀	22.1(70)	24.7(325)	28.6(243)	33.5(103)	33.8(37)	36.9(8)
♀ or ♀	25.6 (5)	28.9 (8)	31.7 (23)	34.1 (23)	35.7(10)	..
Mouth of Elbe for comparison, EHRENBAUM and MARUKAWA (4)						
♂ or ♂	14.5(84)	19.3(141)	24.8(114)	30.9(190)	35.3(28)	38.8(3)
♀ or ♀	..	..	26.0 (8)	33.8 (75)	39.3(21)	44.5(4)

the Dutch and the German samples. My eels of this age were mostly taken in June and in September (especially in the latter month) and even if we assume them to be four years old, to bring them into line with the German age determinations, there remains a difference of nearly 3 cm. This may be explained firstly by the fact that I found only 70 specimens of this age, whereas the German experts had double that number at their disposal, but secondly because eels of less than 20 cm. were very scantily represented in my material, so that the average length of this year group is obviously too high.

If we proceed to distinguish between the catches of various kinds of fishing gear in the Zuiderzee (details of which are not given here), it is at once obvious that some implements catch larger, though not older, eels than other ones.

This may be seen from the following table:—

Table III. Average length and age (in completed years) of eels (all males or of undefined sex) caught with different gear.

Locality and date	Instrument used	Length in cm. at age			
		3 years	4 years	5 years	6 years
Zeeburg near Amsterdam 22. Sept. 1920	eel set nets	23.7 (16)	26.2 (39)	29.1 (23)	35.0 (5)
Between Schokland and Knar 22. Sept. 1920	small trawl ("kwakkuil")	24.3 (16)	27.3 (42)	30.5 (34)	..
Outer Y 13. Oct. 1920	hooks and line	29.2 (4)	32.4 (28)	34.0 (46)	36.3 (10)

It is at once apparent that hooks (generally baited with shrimps) get on the whole larger eels than other implements do, though these eels are of the same age. With eels of 4 years of age there is a difference of not less than 6 cm. between specimens taken with eel set-nets and those caught on hooks in nearly the same water, three weeks afterwards. Is must be, then, of importance to take the implement used into account, if we wish to determine the age of eels in any water. Small trawls ("kuilen") in the Zuiderzee and set-nets ("fuiken") catch indiscriminately, without selection, but it is individuals of rapid growth in each year-group that as a rule fall victims to bait. Silver eels on the other hand are not allured by baited hooks, as they are known to be little inclined to take food.

The eels of the Zuiderzee are mostly 3—7 years old, and those of 4—5 years of age are the most numerous. Those of 3—4 years form by far the larger part of the small eels used for transplanting.

B. Waddenzee.

In these waters some eel fishing is carried out, but the variety of gear is far less than in the Zuiderzee; as a matter of fact only set-nets and bobs are used. Age assessments of various samples, in all containing 566 specimens, during the summer months have given the following data on the rate of growth.

Table IV. Average growth of eels in the Waddenzee.
(Age given in completed years).

Sex	Length in cm. after					
	3 years	4 years	5 years	6 years	7 years	8 years
♂ or ♀	21.9(27)	24.5(202)	27.2(128)	32.8(28)	36.7(23)	..
♀ or ♀	23.7 (3)	25.6 (66)	29.8 (73)	35.4(14)	(2)	..
East Frisian coast, MARCUS (14) for comparison						
♂ or ♀	..	28.8(109)	30.6(117)	..	..	..
♀ or ♀	..	29.8 (38)	31.3 (36)	..	..	..

Along the East Frisian coast the growth rate seems to be more favourable than in the Dutch Waddenzee, but MARCUS (14) sometimes found a less rapid growth in some of his samples.

A comparison of the growth rate of eels from Waddenzee and Zuiderzee (see Table II and Fig. 1) shows that on the whole there is only a

slight difference; the area now under consideration is, however, remarkable, as has been sufficiently pointed out in the first section, for the much greater numerical proportion of undoubted females. Comparing the growth of these we see at once that they outreach the males (or those of as yet undefined sex) in each year-group by at least 2 –2.5 cm. — a phenomenon now well known in the biology of the eel.

All the specimens were taken on or near the extensive eelgrass areas (Zostera) south of Terschelling, with the exception of a small sample from Oudeschild (east coast of Texel). A selection between eels caught either with set-nets or with bobs could not be made in the majority of cases.

C. Hollandsch Diep—Haringvliet.

These waters yield a great many small eels, mostly caught with traps (generally baited with smelt or young herring) of the grig pattern; these implements are attached to a main warp. In autumn large silver eels, putting to sea, are fished with stow-nets, but the catch, hailing from all sorts of localities in the Rhine and Meuse or their tributaries, cannot be considered to represent the real eel population of the particular area now under consideration.

In the period 1920 -1922 I examined 799 specimens, all taken with the first named device. The growth rate is shown in the following table.

Table V. Average growth of eels in Hollandsch Diep and Haringvliet. (Age given in completed years).

Sex	Length in cm. after						
	2 years	3 years	4 years	5 years	6 years	7 years	8 years
♂ } or ♀ {	17.6 (19)	20.5 (333)	23.4 (260)	27.4 (85)	29.1 (10)	(1)	(1)
♀ } or ♂ {	. .	21.1 (7)	25.4 (23)	30.0 (42)	33.0 (17)	(1)	. .

Comparing these figures with those of Zuiderzee and Waddenzee (see Tables II III and Fig. 1) the rate of growth seems excessively slow. Eels of 3 and 4 years, at least the "males", are about 1.5 cm. smaller than those from the northern districts. But more striking perhaps is the fact that males of 6 years of age in their last summer before being taken have only increased their length by 1.5 cm., whereas eels of this age in the other waters have grown to a length of 33 cm., having added about 5.5 cm. to their length in their last complete summer. This retardation of growth in eels downstream may perhaps partly be explained

by the lack of silver eels (not caught in the device used), partly by the small number of specimens of 6 years of age, but we may more readily assume that the large eel population in the mouths of the river does not get sufficient food in these broad entrances of the sea, continually swept by strong tides.

D. Waal (near Nymegen).

In this river eels are largely caught with stow-nets in autumn. My only sample (of July 1920) was taken, however, by grigs and contained 96 specimens; the year-groups are given in the following table.

Table VI. Average growth of eels in the Waal (near Nymegen). (Age given in completed years).

Sex	Length in cm. after		
	3 years	4 years	5 years
♂ } or ♀ {	21.5 (20)	24.3 (55)	25.8 (6)
♀ } or ♀ {	..	25.6 (8)	31.7 (7)

The growth is here slightly better than downstream, in Hollandsch Diep and Haringvliet "males" of 4 and 5 years of age differ but little in length, but this may be due to selection of the smaller specimens.

E. Inland Waters.

To the general reader, not interested in local conditions of limited and isolated areas, the growth of eels in inland waters is of little importance. In order to show the growth in a single locality, in which small eels from the Zuiderzee have been transplanted but which also must contain a certain amount of eels which have immigrated on their own account, the condition of growth in the "Noord-Scharwouder Polder" near Alkmaar is given here.

Table VII. Average growth of eels in the "Noord-Scharwouder Polder" (Age given in completed years).

Sex	Length in cm. after			
	5 years	6 years	7 years	8 years
♂ } or ♀ {	33.7 (23)	34.6 (25)	(2)	..
♀ } or ♀ {	36.1 (61)	38.2 (66)	41.5 (8)	(1)

Two samples, from July and October (1922), were investigated, in all 186 specimens, 73 per cent. of which were females. In May of the preceding year small eels from the Zuiderzee had been imported; these had an age of 3—4 years. At the time of my investigation such transplanted eels should have had one growth zone more in their otoliths. Eels of 4 growth periods did not occur in the material, but those of 5 did, and in this group transplanted eels must be represented to a greater or less extent. Now it is remarkable that eels of the latter age exhibit a favourable growth: 5 cm. more than in the Zuiderzee. Conditions, then, must foster the growth in a remarkable degree. But more striking is the fact that in this age-group 73 per cent. of females are present, and, even if these are not all originally transplanted, there is some indication that freshwater and perhaps plenty of food supply has some influence on sex, assuming that practically all the small eels from the Zuiderzee as used for transplantation are "males", as has been stated in section I. In this case the change or rather the fixation of sex must have taken place in the course of two summers, 1921 and 1922. A definite proof of this interesting problem cannot here be given, as an access to the water (only a small sluice, mostly kept closed for the rest) nevertheless does exist.

It is also curious that real males of six years (in their seventh summer) have not increased their lengths appreciably since the preceding complete growth-period (only 1 cm.); we may ascribe this retardation to their developing into silver eels. After reaching the age of this stage in life males grow but little more but are accumulating an amount of fat in their tissues. That males in their seventh summer as a rule enter the ripening stage will be discussed in section IV; among the eels of the "Noord-Scharwouder Polder" silver eels unfortunately were not represented.

F. Investigation of Scales.

It would seem that the scales of the eel are much more useful for age determination than the otoliths, as the first are easy to be got and generally show growth zones much more clearly than do otoliths.

As has been said GEMZÖE (6) was the first to make use of such scales, and many authors after him, among them JESPERSEN (12) quite recently, though utilising otoliths likewise, have based their growth curves on this method. It must be readily admitted that with large eels, such as have been generally available, this method is the only one to which to have recourse. But the whole question is whether the eel gets its first scales in a definite year of its existence, and EHRENBAUM and MARUKAWA

(4), and later MARCUS (14), have shown conclusively that this is not the case. The first appearance of such scales is dependent not so much on age as on a certain length of the individual eel, generally 16—18 cm., though it is true that such a length in most cases is attained in the fourth summer; (not in the third as GEMZÖE thought); meanwhile cases of scales appearing in the third, fifth or even sixth summer are not unfrequent. To this another difficulty is added, to which MARCUS drew attention: eels of greater age than, say, six years, often exhibit a difference in the number of growth-zones on otoliths and on scales which is greater than 3, so that it is not unlikely that in after years scales, especially the older ones, become deciduous and are replaced by younger ones. In such cases the scales turn out to be nearly valueless for our purpose[1]).

In the summer of 1920 I examined in 600 eels both scales and otoliths, in order to test my age determinations. The results are seen in the following table:—

Table VIII. First appearance of scales in eels at certain age.

Scales appear in	Zuiderzee	Hollandsch Diep, Haringvliet, Waal
2nd summer	..	0.3 per cent.
3rd —	14.0 per cent.	7.0 —
4th —	68.3 —	70.0 —
5th —	16.5 —	19.9 —
6th —	1.2 —	2.5 —
7th —	..	0.3 —

In the Zuiderzee eels grow somewhat more rapidly than in the southern districts and in the rivers, for already 14 per cent. of the small eels in the first named locality had attained the "scale size", if we may put it this way, against half that percentage in the other waters, in their third summer. MARCUS has found a similar fact in comparing growth of eels from the Havel with those from the mouth of the Elbe.

Again, in the southern waters there is rather greater retardation of this first appearance of scales than in the Zuiderzee. All this points to the fact already revealed by the examination of otoliths: in the Zuiderzee eels show a more favourable growth than elsewhere.

[1]) ALM (8) is inclined to explain the difference of more than 3 growth zones in otoliths and scales in the case of Swedish eels by their staying longer than usual in coastal waters before migrating upstream, but this seems to me, as also to WULFF (22), a much more hypothetical assumption.

Section III. Relation between length and weight.

We may ask whether or not the rate of growth may better be gauged y weight than by increase in length, as weight is much the more im- ortant factor to the fisherman. From a biological point of view, however, ve cannot very well rely on it, for weight depends to a large degree on eason, contents of stomach and, as MARCUS (14) tells us, also on sex, s at each length males outweigh females; only in the German Wad- enzee the reverse appears to be the case.

Only the Dutch Waddenzee yielded a sufficient number of both exes to test the truth of MARCUS's statement. It appeared that up o a length of 32 cm. at each centimetre length the weight of females vas slightly more than that of males, which agreed with the conclusions f the German author at the East-Frisian coast. At 32 cm. length nd upwards, however, the males outweighed the females by some —10 grammes; this may be explained by the males, though retarding heir growth on nearing the ripening stage, accumulating fat in their issues and so increasing their individual weight.

For the Zuiderzee and the southern districts such comparisons etween sexes could not be made, on account of the females being too canty. For the sake of brevity the actual figures are not here given.

Another question is the index of quality in eels. We know that with laice there is a simple relation between weight and length

$$\left(w = k\,\frac{l^3}{100} \quad \text{or} \quad k = \frac{100w}{l^3}\right),$$

n which w is weight, l is length and k the said index which ractically may be put $= 1$, but varies according to season. In my el material only the males up to 28 cm. in length were sufficiently umerous to allow the assessment of k. This index, then, turns out to e 0.08—0.12 in spring and early summer and to reach a maximum n early autumn, end of August and September, viz. 0.13—0.14. There s, however, a slight difference in this index according to the waters in vhich the eels were caught, inasmuch as k, taking the whole summer ogether, in males is as a rule highest in the southern districts (Hol- andsch Diep and Haringvliet) viz. 0.123, while in the Zuiderzee this ndex is 0.120 and in the Waddenzee only 0.117. Comparison of Tables II, V and V shows that in the mouth of rivers the rate of growth in regard o increase of length is less than in other Dutch waters, so that it would eem that eels in the southern areas make up for this deficiency in growth y a somewhat greater weight.

Section IV. Age of Silver Eels.

EHRENBAUM and MARUKAWA (4) who investigated eels in winter are of opinion that males do not get their migrating dress before the completion of the sixth summer after metamorphosis, the great majority of them reaching this stage of life in the seventh to the ninth summer.

My own researches point to the same conclusion: out of 44 male silver eels from the Zuiderzee, caught in the autumn of 1920 and 1922, only one individual was in its sixth year, 29 were in their seventh, 12 in their eighth and two in their ninth year. Of male silver eels from the Waddenzee, in October 1921, in all 31 specimens, 10 had completed seven summers and 21 eight.

We may, then, assume that male eels as a rule migrate to sea after having completed their seventh or eighth summer.

This general rule may also be applied to inland waters. I examined a sample of silver eels (all males) caught in the river Dieze near 's-Hertogenbosch, in the beginning of October 1920. With one exception all individuals in the seventh to ninth year (36 of the seventh, 43 of the eighth and 7 of the ninth year — 86 specimens in all) had put on the bridal dress, and also 3 of the sixth year, while 5 others of this latter age did not yet show any sign of the approach of the mating stage. A sample of 16 male silver eels from the "Noord-Scharwouder Polder" near Alkmaar, in October 1922, showed the following ages: 3 of the sixth, 11 of the seventh and 2 of the eighth year.

The lengths of male silver eels varied according to my investigations from 30—42 cm.[1]) which seem to be the extreme limits, judging from the results of similar observations in other countries, although greater lengths have been occasionally recorded. NORDQVIST (8) found 48, HORNYOLD (11a) 51 cm. to be the maximum length, but we may safely say that 42 cm. is the real limit; among a material of no less than 3445 males MARCUS (14) could only find 7 individuals with lengths exceeding this measure (44—49 cm.).

As the males remain small and only attain a maximum weight of 90—100 grammes, their individual value is much less than that of the females, were it not for the fact that in suitable localities they greatly outnumber the latter sex.

JESPERSEN (12) published age determination of a sample of English

[1]) Once a single individual from the Zuiderzee attained a length of 47 cm. REDEKE (17) examined in October 1906 104 silver eels from the Zuiderzee (length from 30—42 cm.) and the present author investigated 60 of such eels (31—38 cm. length) in October 1920, likewise from the Zuiderzee. In both samples all individuals were males.

eels (Norfolk, St. Benedict's Abbey) caught in December 1920 and containing both sexes. Scales were generally used, on account of the large size of the eels, otoliths being only examined in 50 spec., but the author does not state whether the results of both methods tallied or not, nor do we get information whether at least the majority of the males (length 29—45 cm.) had put on their migrating dress, though obviously having regard to the advanced season being prevented from migrating. These males belonged to age groups III—VIII, mostly to groups V—VII, and assuming that they got their scales in their 4th summer, this means that they were from 6 to 11 years. It has been stated above that in Dutch waters at least the highest age of males was 9 years, but either the English eels may get their scales earlier in life or the scale method is not so reliable as those of otoliths. Moreover we must remember that in later stages of life the difference between rings on scales and otoliths may be more than 3, so that the age of these older male eels of JESPERSEN in such a case might be more than 11 years.

The average length of each single year-group in which a sufficiently large number of individuals is examined (groups V—VII) ranges only from 34.4 to 35.8 cm. which confirms the statement made by me that males when nearing their maturing stage grow very little in length.

Female silver eels are as a rule much larger and older than males and they can be distinguished in a sample of such eels already by their larger size (more than 42 cm.), while their weight may be anything from 250 grammes upwards. Females enter their ripening stage probably not earlier than after the tenth summer, but circumstances may retard this till a much greater age. I have, however, paid no special attention to this subject, my chief aim being the investigation of the males which abound in such great number in estuaries. Migrating females originate from all sorts of inland localities, so that it is impossible to tell the particular area in which they have stayed before migration.

Résumé.

Sex determinations in fresh water eels of Dutch waters re-affirm the general rule in the local distribution of males and females. The Zuiderzee practically yields nothing but males, but the Dutch Waddenzee shows even among smaller eels of a maximum length of 27 cm. a rather large percentage of females, which fact is as yet unexplained. Small Zuiderzee-eels of at most 25 cm. length in all about 80 specimens — so far as tests and experience go all males — were reared during three years in a concrete tank filled with running fresh water; after one year

all those examined turned out to possess typical Syrski gonads, but again two years afterwards the remaining individuals, 14 in all, had developed true ovaries. Such experiments, which alone are able to prove Grassi's contention about the sex of the eel not being fixed until after a lapse of years, should be continued, and also glass-eels should be reared likewise under different conditions of life.

The growth of eels, at least of males or those of as yet undefined sex, proved to be somewhat better in the Zuiderzee and the Waddenzee than in the mouths of rivers (Haringvliet, Hollandsch Diep), but the best growth is found in inland waters (Noord-Scharwouder Polder near Alkmaar etc.). My age determinations were made throughout by the aid of the otolith method, which in 600 cases were tested by scale investigations.

The weight of eels of the same length differed according to sex, so far as the weighing of a sufficient number of individuals throughout the summer months can be trusted; the females proved to be heavier than males up to 32 cm. length, which agrees with Marcus's statement regarding eels along the East-Frisian coast.

Male silver eels in all waters investigated had completed their sixth to ninth summer after metamorphosis; generally such male eels migrate to sea at the end of the seventh or eighth summer. Apart from very rare exceptions males reach a maximum length of 42 cm. and this fact enables a separation of the sexes among silver eels to be easily made, females being much larger and older than males.

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The Fleetwood Exploratory Voyages for Hake.

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The object of the exploratory voyages was an endeavour to extend the areas available for hake trawling, and so give some relief to the more heavily worked fishing grounds. The voyages were organised by the Fleetwood Fishing Vessel Owner's Association, and financed jointly by that Association and by the Development Commission, a grant for the purpose having been obtained at the instigation of the Ministry of Agriculture and Fisheries.

The steam trawler "Florence Brierley" was taken over as she returned from an ordinary fishing voyage, and fitted with certain special equipment, including a winch said to be the largest ever fitted on a commercial vessel, capable of carrying 1,500 fathoms of warp on each drum, and a great quantity of spare trawls and otter boards, besides 2,200 fathoms of spare warp. Other equipment included a steam sounding machine, lent by the Fisheries Department, a chronometer, lent by the Admiralty, and Negretti and Zambra reversing thermometers.

Besides her crew, the ship carried a navigating officer, an advisory fishing skipper, a representative of the Fleetwood owners, and the writer as naturalist.

The ship sailed on Tuesday, March 22nd. Her course may be followed on the Chart, Figure 1. A departure was made from the Butt of Lewis, in dull and cold weather, on the morning of March 24th. Fishing was commenced at 5 p. m. on the afternoon of the same day, the trawl (of the Vigneron-Dahl type) being shot in 195 fathoms and hauled in 365 fathoms. From this point the ship worked eastwards along the edge of the deep water of the Faroe Shetland Channel, trawling by day, and usually steaming to the next station at night. The depths worked ranged from 89 fathoms to 560 fathoms.

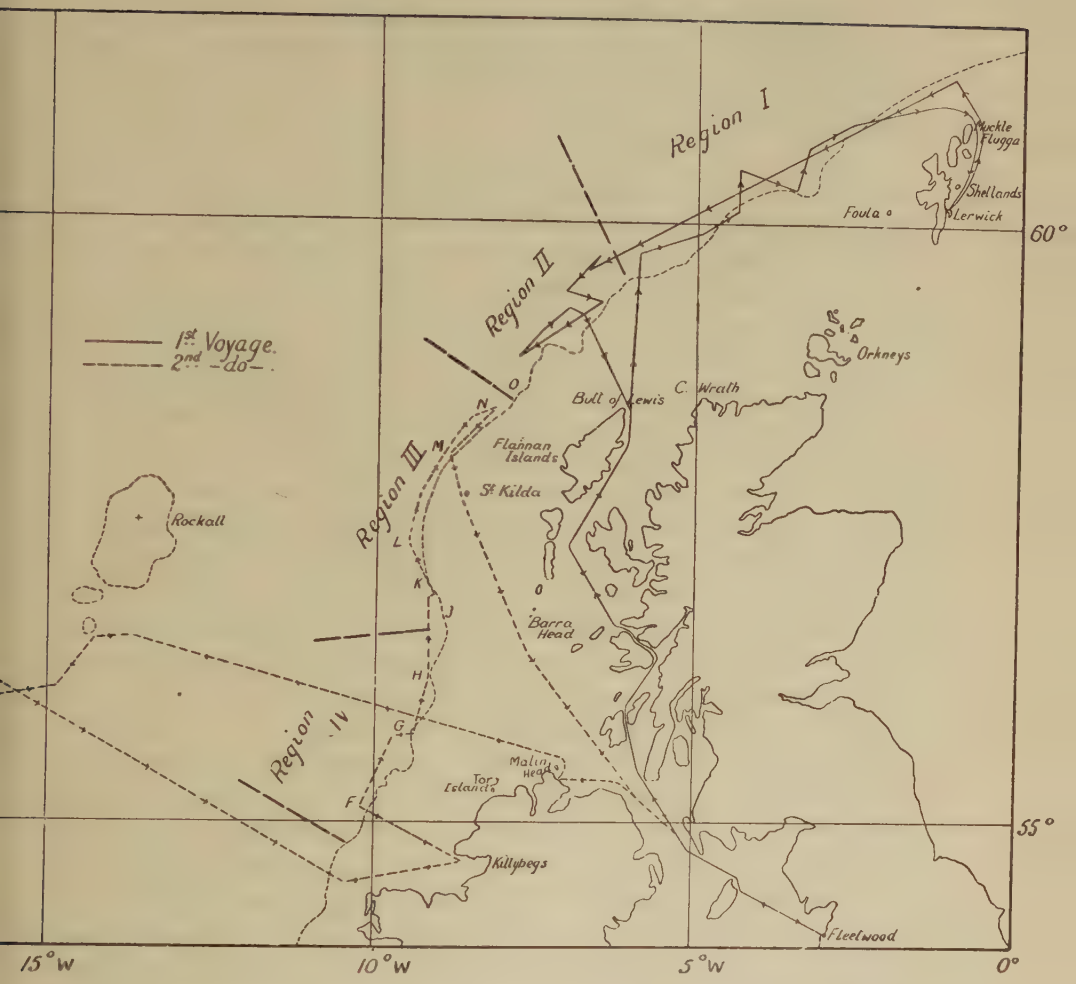

Fig. 1. The approximate cource of the *Florence Brierley*. The Boundaries of the four regions, discussed in the text, are given. F—O are the approximate positions of the hydrographical stations.

The deeper water in the Faroe Shetland Channel proved very barren of fish life. Only 28 species of fish occurred in the catches; but even more impressive than this was the actual quantity of fish taken. Time after time the cod end would come up so empty that it could be hauled aboard by hand, giving perhaps two baskets full of fish, or even less, for a two hour haul. None of the members of the crew had ever seen poorer fishing. The most abundant species were the Coalfish (*Gadus virens*) and the Spur-dog (*Acanthias vulgaris*).

The Vigneron-Dahl type of trawl is unsuited to giving a sample of the bottom fauna, but the coral *Lophohelia prolifera* and the sponges *Phakellia* and *Poecillastra* were very abundant in places, and caused much damage to the gear.

An experimental haul of $1^1/_2$ hours duration was made, the trawl being shot in 505 fathoms and hauled in 560 fathoms, with 1000 to 1075 fathoms of warp paid out from the winch. Only three fish were taken, namely, one *Lycodes Esmarckii*, which came aboard very much alive and lived for some time, and two small specimens of *Raia hyperborea*.

This fruitless exploration of the deeper waters of the Faroe Shetland Channel continued until March 31st, when a point had been reached roughly N. by W. of Muckle Flugga. Only occasional specimens of hake were taken, with the exception of a haul in 100 fathoms N.W. of Foula, when a score of hake were caught in a $2^1/_2$ hours tow. We learned later that Aberdeen trawlers were catching a certain quantity of hake in this locality. These hake were found to be feeding on herrings, and apparently also on mackerel, and, as the herrings were spawning at this time, the small concentration of hake, indicated by this haul off Foula, would point to a local concentration caused by feeding on these herrings. The fact that, even so, only one score of hake were caught in $2^1/_2$ hours, might perhaps be regarded as additional evidence of the scarcity of hake in the Faroe Shetland Channel.

Herring spawn was found in the stomachs of *Gadus virens* (coalfish) as far west as Lat. 60°08′ N., Long. 4°17′ W.; it occurred in increasing quantities in the stomachs of these fish as we worked eastwards, until in Lat. 60°18′ N., Long. 3°30′ W., as much as 120 grams of spawn were found in a single stomach. At this last station the eggs were developing, and the eyes could be clearly distinguished. As stated in the previous paragraph, female herrings in stage VI (i. e. actually running) were caught off Foula, and finally, in approx. Lat. 60°40′ N., Long. 3°20′ W. a considerable quantity of herring larvae were taken 20 metres below the surface, at midnight, with a plankton net. The greatest depth of haul from which coalfish, containing herring spawn, were taken, was in a haul shot in 195 fathoms and hauled in 365 fathoms, but the greatest quantity of spawn was found in fish taken in a haul shot in 150 fathoms and hauled in 115 fathoms. Since the sea bottom slopes very steeply however, at these depths, so that it is but a short distance from 100 fathoms to 200 and 300 fathoms, the spawn found in the stomachs of these fish need not have been deposited at as great a depth as that at which the fish were caught.

In this region also a specimen of the Greenland shark, *Somniosus*

microcephalus (Schneider) Goode and Bean, 3.4 metres in length, was taken in a haul shot in 295 fathoms and hauled in 340 fathoms. The temperature was 8.4° C. The stomach contained the remains of ling.

On March 31st the ship steamed into Lerwick, to take aboard some thermometers which had been ordered by wireless.

After a discussion, it was decided to try no further to the eastward. Hake was known to be present in quantity in the Norwegian Deep Water, but the fact that we had only found very small quantities of scattered hake in the Faroe Shetland Channel convinced us that there was no continuous distribution of hake between the Norwegian stock and the main Atlantic Slope stock. Having regard to the time already spent, and the supply of coal and provisions, it was decided to return to the western side of the Wyville Thompson Ridge.

Accordingly, after one more haul in 90—102 fathoms due north of Muckle Flugga Light, the ship steamed away on a course W. by S., and at 3.45 p. m. on April 3rd the trawl was shot in 135 fathoms on the western slope of the Wyville Thompson Ridge (Region II, Chart I), and the rest of the voyage was spent working in a westerly and southerly direction along the edge of the deep water. Hake were found in good quantity, and some excellent catches were made. The depths fished ranged from 118 fathoms to 520 fathoms, but the nature of the bottom made working here a matter of great difficulty. This is best illustrated by the fact that 14 of the 32 hauls made in this region were more or less profitless on account of splits, the chief causes of these casualties being stones, and great bushes of the "pudding" sponge *Poecillastra compressa* (Bowerbank).

Fish were much more abundant, both in number of species and in actual quantity, on the western side of the Wyville Thompson Ridge than on the eastern side of the Ridge at comparable depths. It appears that 49 species were taken in hauls from the former region whereas only 28 species were found in the latter region. Of these, 18 species were common to both regions.

A list of the species found is to be published in a separate paper.

The ship returned to Fleetwood with a good voyage of hake aboard, on April 13th.

The second voyage was commenced on the afternoon of April 19th. We ran into bad weather almost at once, and, on the 20th, put into Portaleen, under the lee of Malin Head, and anchored for the night in a hard breeze, with continual squalls of rain. On April 21st we resumed our course for the Rockall Bank, but bad weather continued, with westerly winds, so that the ship was eased down for many hours, and it was not

until Saturday, April 23rd, that the Bank was found with the lead at 150 fathoms. The trawl was shot at this depth and hauled in 240 fathoms.

For the next two days the vessel worked, when weather permitted, round the southern slopes of the Rockall Bank, in depths ranging between 132 fathoms and 285 fathoms. Five hauls were made, and a fair quantity of fish was taken, but no hake.

On the evening of April 24th it was decided that, since there was no sign of hake at this, the warmest and most southerly point of the Rockall Bank, and since the weather was steadily growing worse, we had better abandon further work in this region. We therefore steamed for Donegal Bay. On April 25th it was blowing a full gale from the N.W., and a heavy tumbling sea got up, but towards evening the wind veered to the N.E. and moderated considerably. We picked up Eagle Island Light at 10 p.m. and anchored in Killybegs Harbour, Co. Donegal, early on April 26th.

On April 27th we steamed out of Killybegs. The programme was now to fish northward along the slope, at depths greater than those usually worked by steam trawlers, partly to try to establish the maximum depth at which it is profitable to fish for hake, and partly to find whether there were any areas suitable for trawling between the well known deep-water grounds W.N.W. of Tory Island, and W. from Barra Head.

This programme was carried out in fairly fine weather, and 54 hauls were made at depths ranging from 120 fathoms to 440 fathoms. The continental slope between Tory Island and Barra Head proved too precipitous to be important for trawling.

May 8th found the ship working N.W. of St. Kilda, where the supply of coal and stores compelled us to abandon further work. We returned to Fleetwood on May 10th.

In all, 31 days were spent in fishing, and 118 hauls were made: namely 26 hauls in Region I, 33 in Region II, 5 on the Rockall Bank, 35 in Region III, and 19 in Region IV. Of these 118 hauls, 41 were more or less foul, the gear being torn or the bridles broken, or even in some cases, the whole trawl, including the boards, being lost. These figures give a good idea of the nature of the sea bottom on the northern deep water fishing grounds, and of the labour, patience and skill required to work them successfully.

Temperature Observations during the Voyages.

Messrs. Negretti and Zambra's reversing thermometer frame (Admiral Magnaghi's Patent) was used in these observations. The thermometer was graduated to 0.5° C., but the temperature was read to 0.1° C., with the aid of a lens, by eye-interpolation. During the first

voyage, when Regions I and II were investigated, temperatures were taken only at the sea bottom, except, of course, where the lead failed to find bottom; but, during the second voyage, 14 stations were worked from surface to bottom, usually at 100-metre intervals.

The five stations worked over the tail of the Rockall Bank were of especial interest. The position of these stations is given in Figure 2,

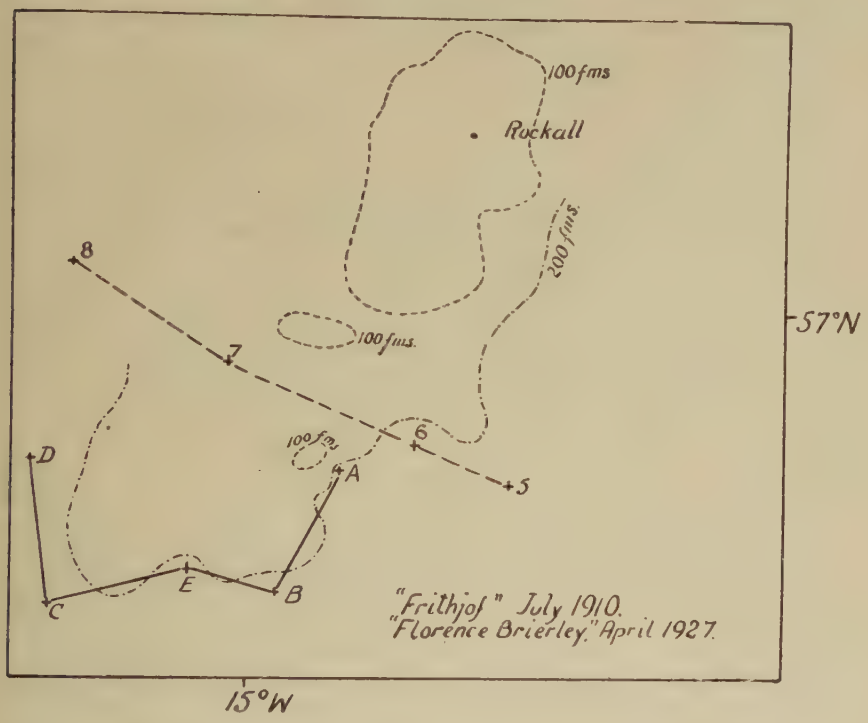

Fig. 2. The 100 and 200 fathom contours on the southern slopes of Rockall Bank. A—E are the positions of the *Florence Brierley* hydrographical stations, April 1927. 5—8 are the *Frithjof* stations, July 1910.

and the hydrographical section obtained is drawn in Figure 3. It appears that the deeper portions of the eastern slope of the bank carry cold water, of a temperature as low as 8.2° C. The western slope, however, carries warmer water, viz. 8.7° C., and there is a well marked tendency for the isotherms to slope downwards steeply towards the west. There is a heaping up of colder water, therefore, on the south eastern slopes of Rockall Bank.

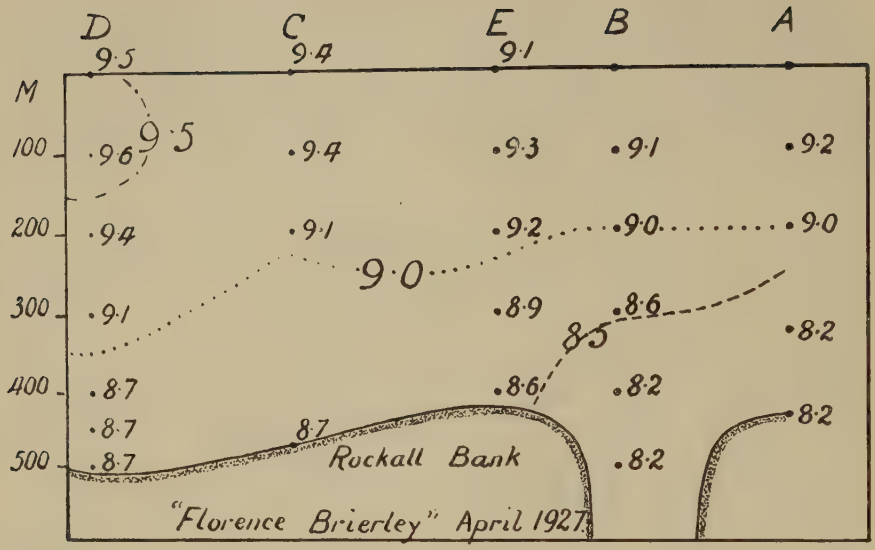

Fig. 3. Hydrographical section of the southern slopes of Rockall Bank. *Florence Brierley*, April 1927. Depth in metres. Stations as in Fig. 2.

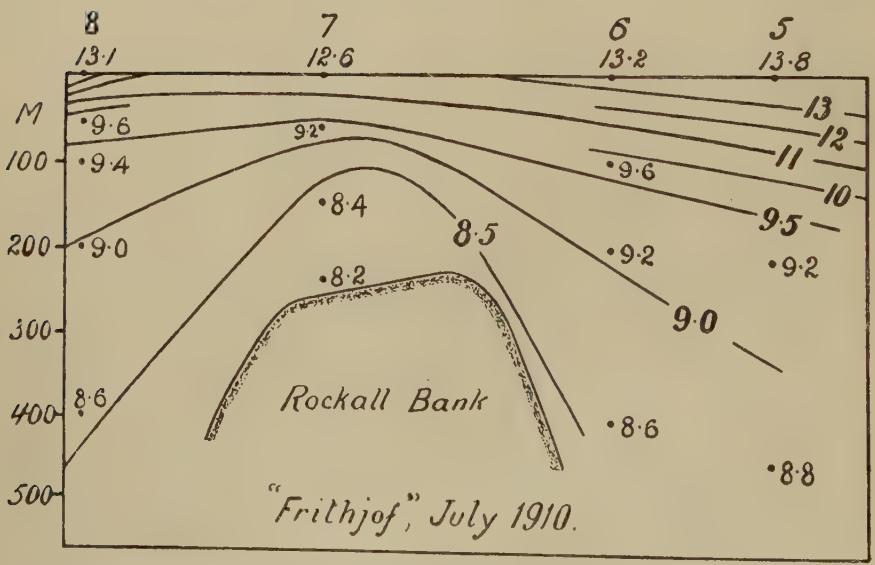

Fig. 4. Hydrographical section of Rockall Bank. *Frithjof*, July 1910. Depth in metres. Stations as in Fig. 2.

These observations agree with the results, published by NANSEN[1]) of the stations worked in this region by the "Frithjof" in July 1910. His stations 5, 6, 7 and 8 are shown on the chart in Figure 2 and the hydrographical section obtained from his data, drawn to the same scale as Figure 3, is given in Figure 4. The presence of cold water on the bank is clearly indicated, but the isotherms, in this case, fall away more or less symmetrically, and there is no indication of a heaping up of colder water on the eastern slopes. NANSEN's *surface* temperatures are much higher than those found by the "Florence Brierley", since the "Frithjof" visited Rockall Bank in July, when surface heating was taking place,

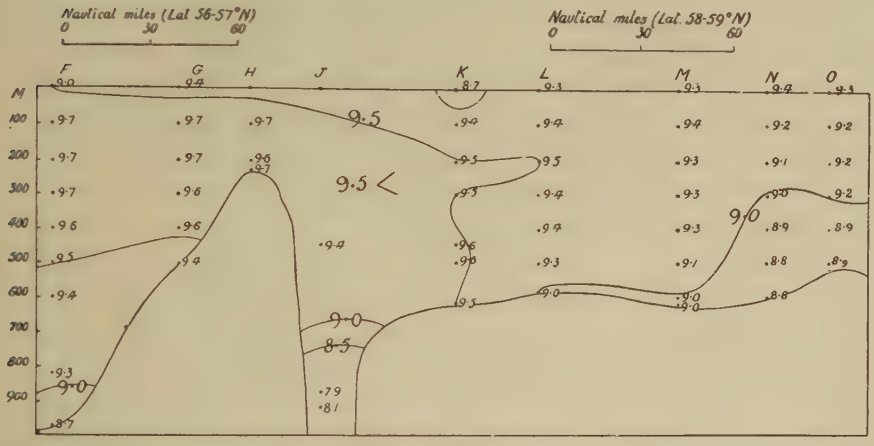

Fig. 5. Hydrographical section along Continental Slope. Position of stations as in Fig. 1. Depth in metres.

but there is good agreement between the temperatures found in the deeper water.

Nine stations were worked along the edge of the deep water, from Lat. 55°07′ N. to Lat. 58°40′ N. The hydrographical section obtained from them is drawn in Figure 5, and the position of the stations is indicated in Figure 1 (F—O). There is strong surface cooling everywhere, which is especially noticeable in the more southerly stations. For example, at station K, when this station was worked, the wind was easterly and the air at 6.2° C.; the water about 1 metre below the surface was 8.7° C., a temperature low when compared with other stations. The section shows the obvious tendency for the water to become colder from south

[1]) The waters of the North Eastern Atlantic. Internationale Revue der Ges. Hydrobiologie u. Hydrographie. Hydrographical Supplement to Vol. IV.

to north and from surface to bottom, but the most important point to be noticed is the great uniformity in temperature. Indeed, the difference between the highest observation, off Tory Island, and the lowest observation, off Muckle Flugga, was only 1.6° C., though these stations are approximately 500 miles apart.

The bottom temperatures found in Region I agree in every respect with the temperature charts published in the Report of the North Western Area Committee for 1924 and 1925[1]). At depths shallower than about 150 fathoms, the temperature at the sea bottom gradually became lower, in the Faroe Shetland Channel, from 8.7° C. at the western end to 8.1° C. at the eastern end, off Muckle Flugga. The deeper water of the channel, however, was much colder, two observations at 300 and 343 fathoms giving temperatures of 6.6° C. and 6.0° C. respectively. The corresponding depths on the western side of the Wyville Thompson Ridge carried water of much higher temperature namely, 8.7° C. to 8.9° C. This phenomenon is very well known.

From the nature of the data, no hydrographical section can be drawn for Region I.

Effect of Depth on the Catch of Hake.

The considerable number of hauls made (118) allows of a quantitative examination of the effect of depth on the catch of hake.

The hauls have been treated in the following way. For every haul, records have been kept of the time of hauling and shooting, and the catch, in scores of big hake, and baskets of "chat hake" (i. e. smaller hake). Now, a number of counts showed that an average of 10 fish per basket would give an approximately correct figure for the total number of chat hake caught. For every haul, therefore, the number of scores of big hake multiplied by 20, and the number of baskets of small hake, multiplied by 10, added together, give the approximate number of hake caught. This figure, divided by the number of hours, or fractions of hours, during which the trawl was on the bottom, gives the catch per hour.

The hauls have been grouped, according to their mean depths, in 20-fathom categories, and for each category the mean catch per hour has been calculated. The "mean depth of haul" is the mean of the depths at which the trawl was shot and hauled respectively. It is the only figure, representative of the depth at which the trawl has been fishing, which

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[1]) J. P. Jacobsen & Aage J. C. Jensen. Rapports et Procès-Verbaux, Vol. XXXIX, May 1926.

one is entitled to assume, but it may obviously lead to error where the sea bottom is very uneven. These data are set forth in Table I, and the curve obtained by "smoothing in 3's" is drawn in Figure 6. Unfortunately, both in very shallow and very deep water the number of hours' fishing is statistically inadequate, but over the greater range of depth the number of hauls is sufficiently large to discount, to a considerable extent, inaccuracies due to splits, foul hauls, and differences in the time of day, as well as those due to an untrustworthy "mean depth" of haul.

Table I.

Variation in Catch of Hake per Hour's Fishing with Mean Depth of Fishing.

n Depth Haul. Iean of ndings Shooting Hauling, athoms.	Regions I and II				Region III				Region IV				Total all Regions			
	No. of Hauls	Hours of Fishing	Catch per Hour	Catch Smoothed in 3's	No. of Hauls	Hours of Fishing	Catch per Hour	Catch Smoothed in 3's	No. of Hauls	Hours of Fishing	Catch per Hour	Catch Smoothed in 3's	No of Hauls	Hours of Fishing	Catch per Hour	Catch Smoothed in 3's
— 100	2	3.0	2.0	..	..	..	..	..	..	..	..	..	2	3.0	2.0	..
< 120	6	12.5	1.9	1.4	..	..	..	..	..	..	..	..	6	12.5	1.9	1.8
< 140	5	7.25	0.3	1.2	..	..	..	..	3	3.25	4.6	..	8	10.5	1.6	2.3
< 160	5	6.75	1.3	0.5	..	..	..	..	1	1.25	14.4	..	6	8.0	3.4	1.7
< 180	1	1.0	0.0	0.7	..	..	..	..	..	..	..	..	1	1.0	0.0	4.7
< 200	3	3.5	0.9	1.2	..	..	..	..	1	1.5	33.3	..	4	5.0	10.6	6.7
< 220	3	3.75	2.7	7.8	..	..	..	..	7	9.75	12.2	81.8	10	13.5	9.6	23.8
< 240	2	3.75	19.7	11.4	3	4.5	44.4	..	1	1.0	20.0	78.3	6	9.25	51.2	28.9
< 260	4	6.75	11.9	44.5	4	8.75	37.7	38.8	3	3.0	22.7	75.9	11	18.5	25.8	55.0
< 280	14	24.0	102.0	47.5	2	3.5	34.3	37.3	2	1.75	5.1	38.6	18	29.25	88 1	52.7
< 300	2	3.5	28.6	80.7	7	12.5	40.0	31.8	2	2.5	88.0	..	11	18.5	44.3	53.2
< 320	4	7.75	51.6	45.1	14	30.5	21.1	27.0	..	..	..	..	18	38.25	27.3	31.7
< 340	1	2.0	55.0	43.2	4	8.5	20.0	..	1	2.25	8.9	..	6	12.75	23.5	24.1
< 360	3	5.25	23.1	45.3	..	..	..	..	1	1.75	17.1	8.7	4	7.0	21.6	25.2
< 380	1	2.25	57.8	27.0	..	..	..	..	1	2.0	0.0	7.4	2	4.25	30.6	22.4
< 400	..	..	..	(19.3)	1	2.0	25.0	..	1	2.0	5.0	..	2	4.0	15.0	(15.2)
< 480	1	1.75	0.0	..	..	..	..	..	..	..	..	..	1	1.75	0.0	..
< 520	1	1.0	0.0	..	..	..	..	..	..	..	..	..	1	1.0	0.0	..
< 540	1	1.5	0.0	..	..	..	..	..	..	..	..	..	1	1.5	0.0	..

The maximum catch of hake per hour occurred at 260—280 fathoms mean depth (at 240—260 fathoms in the smoothed figures) and from this depth the catch per hour decrease both towards shallower and deeper water. A surprising fact is, that at a mean depth of 380—400 fathoms there was still, apparently, an appreciable quantity of hake, but at the next depth-category for which a figure is available, viz., 460—480 fathoms, no hake were taken.

The two deepest hauls, in which hake were caught, were shot in 247 and hauled in 520, and shot in 350 and hauled in 425 fathoms respectively.

If these figures are to be considered reliable, this means that hake may be caught on the northern grounds as deep as trawlers can fish with their present equipment. Needless to say, there is very great seasonal variation in the optimum depth for hake.

In figure 6 there is also inserted the curve for the variation of catch with depth in Regions I and II, which include the new extension of the

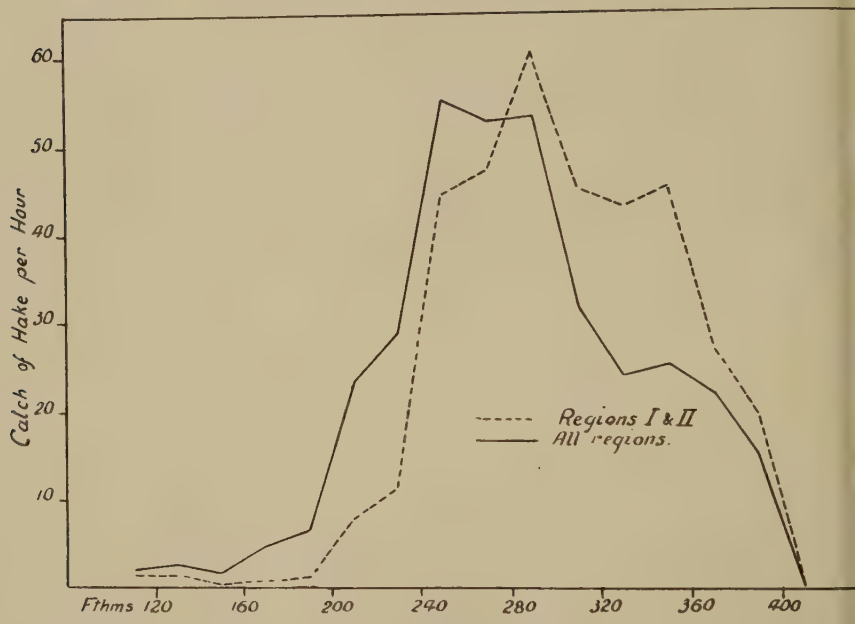

Fig. 6. Variation in catch of hake per hour, with increase of depth, in Regions and II, Fig. 1, and in all regions. Depth in Fathoms. Catch in Number of hak per hour. Data in Table I.

hake grounds. It is seen that the peak is reached at 260—280 fathom (280—300 in the smoothed figures).

COLLETT[1]) (1896) states that the "Travailleur" and "Talisman" caught hake at 640 metres (350 fathoms) off Cape Bojador (Sudan) and GOODE[2]) (1881) states that the hake has been recorded from depth of 115 to 487 fathoms on the edge of the Gulf Stream off the New Englan coast.

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[1]) Campagnes Scientifiques. Monaco. X, Poissons.

[2]) Proc. U. S. National Museum. Vol. III, 1881.

Effect of Temperature on the Catch of Hake.

It seemed worth while to make as extensive observations as possible on the temperature of the sea bottom, in order to discover if any relation could be found between the temperature there and the catch of the hake.

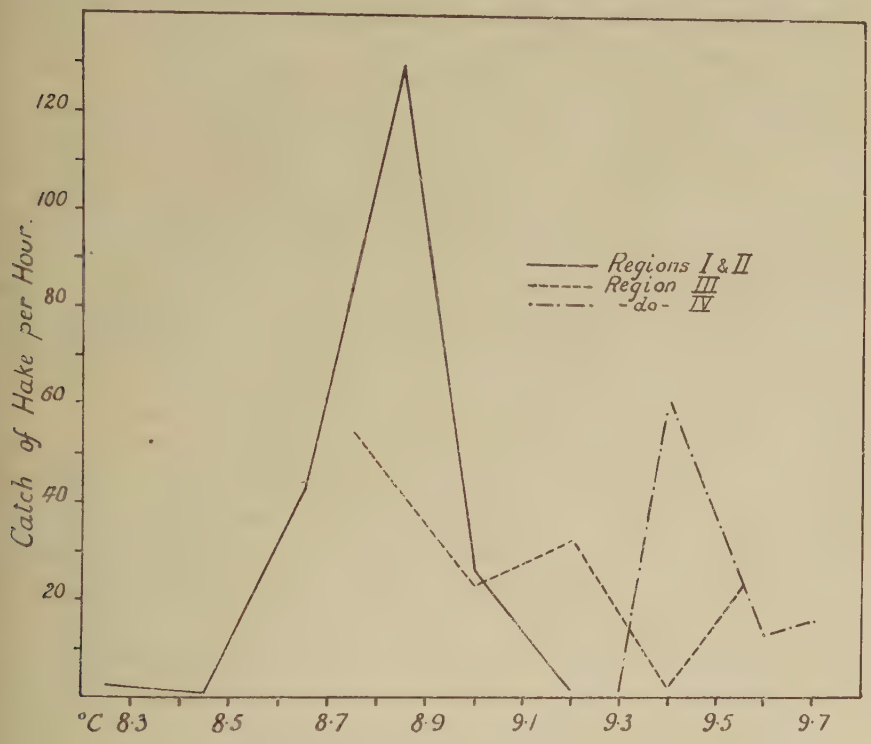

Fig. 7. Variation in catch of hake per hour, with temperature, in Regions I and II, III, and IV, respectively. Temperature in degrees centigrade. Catch in numbers of hake per hour.

An observation was made at almost every sounding. The improvised instrument used during part of the voyages is described elsewhere[1]).

The figures for catch of hake per hour were obtained in the same way as in Table 1, and give the mean catch of hake per hour for each 0.1° C. The figures for Region I and II, Region III, and Region IV, have been worked separately, and the three curves are shown in Fig. 7.

[1]) Journal du Conseil. Vol. II. No. 2. 1927.

In Regions I and II, there is a definite crest shown in the curve for variation of catch with temperature, such that the largest catches were made at 8.8—8.9° C. The catch is almost nil from 8.2° to 8.6° C., and then there is a sharp rise to the maximum at 8.9° C., after which the catch per hour falls away again.

In Region III hake were caught most abundantly at about the same temperature as in Region I and II, namely, 8.7—8.8° C., and there was a marked tendency to a falling off below this temperature, though the curve is irregular.

In Region IV no hake were taken at a temperature below 9.4° C. This temperature was the optimum, after which catches fell away once more.

The writer feels that the results of this comparison of catch of hake with temperature may be taken as indicating that further work with a more sensitive thermometer, graduated to 0.1° C. and reading, say, from 6° C. to 16° C. is very desirable and might give more promising results. The difficulty lies in the very slight differences in temperature at different depths over a wide area. This has already been referred to.

The Food and Feeding of Hake.

The main portion of the work done on hake during the voyages was the routine weighing and measuring of the whole fish, and of its liver and gonads. The results will be published in a future paper, with those of the rest of the writer's voyages on commercial trawlers. The food found in the stomachs of these hake was examined, and it was at once evident that the Blue Whiting (*Gadus poutassou*) was by far the most important item of food. Whereas 20 specimens of all other species were found, no fewer than 434 specimens of blue whiting were found in the stomachs of 955 hake. Only specimens were counted as food which showed definite signs of digestion, and absolutely fresh specimens, which might have been gulped up during the hake's struggles in the trawl, were rejected. The remaining food of these hake included 7 specimens of *Argentina silus*, 3 *Gadiculus argenteus*, 4 herring and 2 mackerel (found in hake caught off Foula) and 4 large specimens of *Scopelus Mülleri*.

If one examines the food found in hake from the various regions, one sees that the quantity of food eaten by hake in Region II is very much greater than that eaten in the other three regions. In order to express this in terms of weight of food per fish, the method, of weighting used in Fisheries Investigations, Series II, Vol. X No. 2, has been adopted. The number of specimens of each species found in the stomachs

of hake is multiplied by a number which represents the mean weight of that species, the result being a figure which represents the total weight of food eaten by a known number of hake. From this, one finds the weight of food per fish by a simple calculation.

On comparing the mean weight of food per fish in the four regions, it is seen that by far the heaviest feeding took place in Region II, where 171.0 gms per fish were found. In Region I there were 46.9 gms per fish, in Region III 30.3 gms per fish, and in Region IV 24.9 gms per fish.

All the hake examined in Regions II, III and IV were spent, or in the earliest stages of recovery, except for a few advanced stages in Region IV; the four regions may therefore be justly compared with one another in the matter of the feeding of hake; and since these hake will tend to have been in their hungriest condition, the quantity of food eaten may be taken as a direct index of the quantity of food available.

It has been pointed out that, except in Region I, blue whiting form the enormous bulk of the food eaten, the quantity of other kinds being negligible. One may therefore deduce that blue whiting were exceptionally abundant in Region II, less so in Region III, and still less so in Region IV.

If one compares these data for food per fish in the four regions (i. e. abundance of food) with the mean catch of hake per hour, it is seen that there is a correlation between these figures. The very high rate of feeding in Region II is associated with a high value for "mean catch per hour" (Figure 8), and the catch of hake per hour in Regions III and IV falls away just as the rate of feeding falls away. In Region I a high rate of feeding, as compared with the rate of feeding in Region III and IV, is accompanied by a very low mean catch per hour, but the total number of hake to be caught in Region I hardly justifies a comparison with the much greater number of fish caught in other regions, and the question of hake in the Faroe Shetland Channel is dealt with in the discussion.

The figures on which Fig. 8 is based may be summarized as follows:—

Region	I	II	III	IV
Weight of Food per Stomach (Hake)	46.9 g	171.0 g.	30.3 g.	24.9 g.
Mean catch of Hake per hour	1.5	62.6	28.7	23.7
Mean percentage of everted stomachs	54.1 %	17.5 %	49.8 %	52.0 %

The quantity of food per fish in Region II is the greatest the writer has ever seen in the deep water hake fishery, and, with the exception of hake feeding on small mackerel and herrings, in shallow water in Galway Bay, (September, 1925), the heaviest he has ever seen.

In the summary of these figures, given above, are also given the results

of counts on the numbers of hake which were found "everted", i. e. with the stomach, turned inside out, forced out of the mouth. This eversion is due to the sudden expansion of the gas in the gas-bladder, on hauling the fish rapidly to the surface. Now, as appears from Figure 8, there is a relation between the extent of feeding and the extent of eversion, such that heavy feeding is accompanied by a low percentage of eversion. It is certain that the ability to prevent eversion, by a rapid absorption

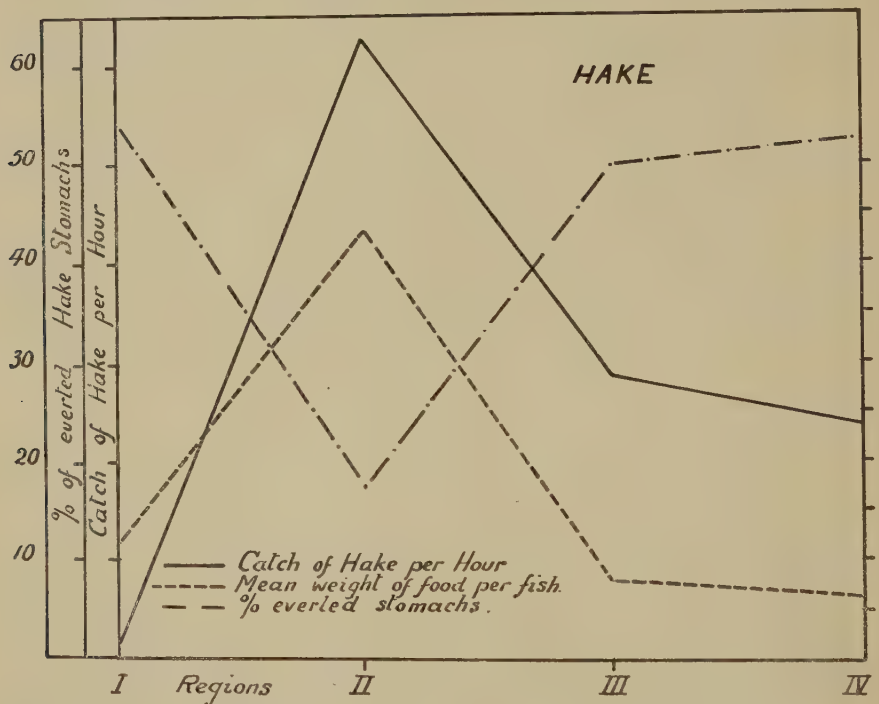

Fig. 8. Curves showing the mean catch of hake her hour, the mean weight of food for fish in hake, and the percentage of everted stomachs, in Regions I, II, III, and IV. Fig. 1.

of the gas, depends on the vigour of the fish. For this reason hake caught in the short hauls customary on the rough northern grounds present a much lower rate of eversion than those caught in long hauls on the fine grounds west of Ireland, since in the former case a greater proportion of newly caught, and therefore still vigorous, fish are present. But from Figure 8 it appears that the explanation, in this case, lies probably in the fact that a fish with a full stomach resists eversion better than a fish with an empty stomach.

Notes on the Blue Whiting.

The great importance of this fish as food for hake warrants a special note. The Blue Whiting was found in all four regions, and on the Rockall Bank. In Region I it was restricted to the western portion of the Faroe Shetland Channel, and specimens were not found in the trawl east of approximately Longitude 4°56′ W., while they occurred in the stomachs of *Gadus virens* as far east as Longitude 4°27′ W.

Evidence for the great abundance of blue whiting in Region II has just been discussed, and for its lesser abundance in Regions III and IV.

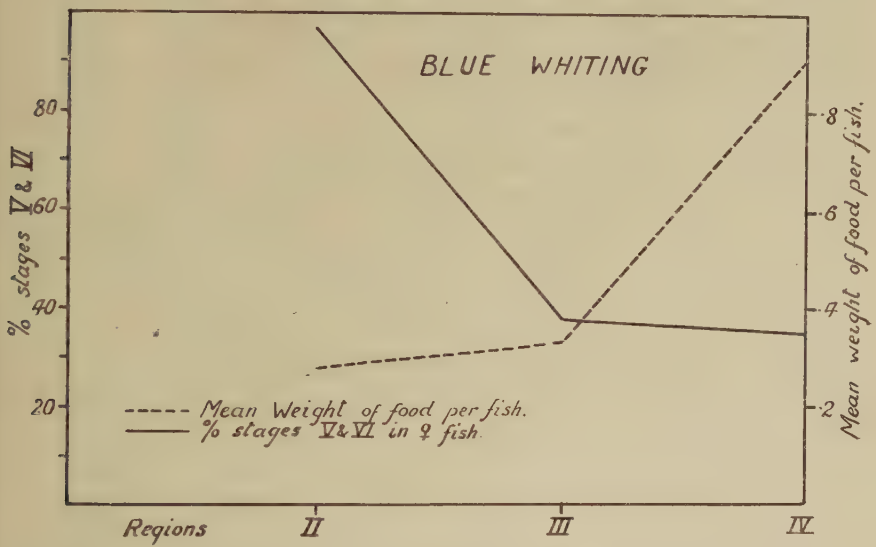

Fig. 9. Curves showing the mean weight of food per fish in blue whiting (*Gadus poutassou*), and the percentage occurrence of maturity stages V and VI among females, in Regions II, III, and IV. Fig. 1.

The blue whiting females in Region II were almost all in a maturity stage corresponding to Hjort's Stage V for herrings, that is, the roe was big, filling a considerable part of the body cavity, while the contained eggs were large and easily visible to the naked eye, though still opaque. A few specimens were met with in stage VI, i. e. with the ovary much swollen, its membrane tightly stretched, and the contained eggs large, and transparent. Still fewer specimens were found in Hjort's Stage VII, i. e. spent, in fact, 96.6 % of the blue whiting females examined in Region II were in Stages V and VI.

In Regions III and IV a more advanced state was shown; here spawn-

ing was almost accomplished. In Region III only 37.4 % of the females were still unspent, and in Region IV only 35 %.

It is interesting to note that, in Region IV, where 65 % of the blue whiting were spent, there was a comparatively high rate of feeding, with an average of 0.9 grams of food per fish.

In Region III there was a low rate of feeding, namely, 0.33 grams per fish, though the percentage of spent fish was high (62.6).

In Region II there was a low rate of feeding, and spent fish were almost absent. These facts are shown graphically in Figure 9, and summarized below.

Region	II	III	IV
Number of ♀ Blue Whiting examined	148	131	103
% of ♀ Blue Whiting in Stages V & VI ..	96.6 %	37.4 %	35.0 %
Number of Stomachs examined	184	187	274
Mean weight of food per fish	0.28 g.	0.33 g.	0.90 g.

It is well known that the feeding function in fishes is inhibited at the time when the roes and milts are ripe; but here there seems to be "lag" in the resumption of feeding, so that in Region III, where there was a high proportion of spent fish, active feeding had not yet been resumed. The blue whiting caught on the Rockall Bank were apparently in the same condition; they were almost all spent fish, but contained little or no food, and appeared meagre and emaciated.

Regions II, III and IV seem to show an interesting progression in the spawning of blue whiting. In Region IV spawning was almost over, and active feeding had recommenced, in Region III also spawning was almost over, but feeding had not recommenced, and in Region II spawning had not yet fully commenced.

About 90 % by weight of the food of the blue whiting consisted of *Meganyctiphanes norvegica* ("Krill"); other organisms included the luminous fish *Maurolicus pennanti*, and young specimens of *Scopelus* sp.

Discussion.

The voyages can be considered a success to this extent, that the deep-water winter hake fishing grounds have been extended northward from off the Flannan Islands to the Wyville Thompson Ridge. On the negative side, they have proved fairly conclusively that the Wyville Thompson Ridge is the northern limit of the Atlantic deep water fishery, and that hake are not met with to the north and east of the Ridge, at

least not in sufficient quantity to attract a hake trawler, until the Norwegian Rinne is reached.

The proportion of the largest and most valuable sizes of hake was remarkably high on the new extension of the grounds, yet, having in mind the very narrow area of the steep continental slope between 260 and 320 fathoms (the optimum depth) and the resulting very intensive nature of the trawling there, one questions whether the hake stock visiting this area can long sustain this proportion of big fish. The relief given can only be regarded as temporary. But the very fact that there has been an extension of the area available for hake trawling means, on the average, less intensive trawling on all grounds and therefore a somewhat improved chance of survival for the hake.

The relatively high catches on the new grounds seem to be associated with the spawning of the blue whiting, the principal food of the hake. Schmidt[1]) shows that, though adult blue whiting are found all over the Norwegian Sea and in the northern North Sea, no spawning takes place to the eastward of the Wyville Thompson Ridge and the Faroe-Iceland Ridge. This clearly implies that, in order to spawn, blue whiting must migrate to the west of these ridges, and the relatively very great concentration of blue whiting found in Region II (chart 1) might perhaps be due to fish from the southern Norwegian Sea reinforcing the local stock of blue whiting during the spawning period. Since these blue whiting, the food of the hake, were also still in the ripe, though unspawned condition, and therefore probably in the densest concentration, these facts go far to explain the high average catch of hake per hour in this region, as compared with other regions investigated.

There is good reason, therefore, to believe that the deep water fishery on the new hake grounds is associated, even more closely than elsewhere, with the spawning of the blue whiting. If this is correct, the season will be found to range from late January to early May, with a maximum early in April.

This may also throw some light on the virtual absence of hake from Region I. The majority of the hake may have moved westwards after the blue whiting, with the exception of those few which remained in the neighbourhood of the Shetlands to feed on the herrings. It is tempting to think that the waters of the Faroe Shetland Channel, especially as one moves eastward, become too cold for hake, and this may be true of the greater depths, such as 300 fathoms, where we found a temperature of 6° C. But the presence of abundant hake in the Norwegian Deep

[1]) Rapports et Procès-Verbaux. Vol. X. 1909.

Water, where, according to the Hydrographical Bulletins[1]), the temperature at 80—100 fathoms is no higher than 8° C. even in May, July and September, and in the deeper portions as low as 6.5° C., weakens this point. The opinion we formed at the time was, that 8.7° C. represents the lowest temperature at which the hake, which is essentially a warm-water species, is found in commercially profitable quantities, and that the Norwegian hake must therefore represent an isolated local stock. This theory will be tested when opportunity offers.

The voyages cannot be said to have definitely disproved the presence of hake on the deeper slopes of Rockall Bank. At one position we found water at 8.7° C., a temperature at which we were getting considerable quantities of hake in regions II and III. The blue whiting is abundant on the Bank.

Hake are abundant on the Porcupine Bank in September, October and November, though at other times of the year they may be quite absent, and a comparison with Rockall Bank is obvious. In the case of Rockall, however, there is a much greater distance between the Bank and the nearest point of the 100 fathom line than in the case of the Porcupine, and Nansen (*loc. cit.*) gives the temperature at 300 and 400 metres (164 and 218 fathoms respectively) on the western slopes of the Porcupine Bank, in the region where the hake are caught, as 9.9° C. Even if it is true that the hake is a midwater fish, independent of the sea bottom for its food, and capable of living over the great ocean depths, one doubts whether any but occasional specimens would wander as far west as Rockall Bank.

It gives me great pleasure to acknowledge here my thanks to Mr. Leech and Mr. Mason[2]), of the Fleetwood Fishing Vessel Owners' Association, for their ready help in recording, and to Capt. Sandham for his practical help, unceasing interest, and for many valuable suggestions.

Summary.

A report is given of the Fleetwood exploratory voyages for hake, March—May 1927. A northerly extension of the hake grounds was found and explored. Hake were rare in the Faroe Shetland Channel, and were not met with on Rockall Bank.

The best catches of hake were made between 260 and 320 fathoms.

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[1]) Especially Bulletin Hydrographique Juillet 1908—Juin 1909. Conseil. Perm Exp. Mer.

[2]) since deceased.

Hake are apparently not present at depths greater than approximately 380 fathoms. The sea bottom on this new extension is extremely rough with stones and coral.

Investigations of the stomach contents of hake showed that the comparatively high catches made on the new grounds were associated with a very high rate of feeding. The Blue Whiting (*Gadus Poutassou*, Risso) was almost exclusively the food of the hake, was apparently present in remarkable abundance, and, at the beginning of April, was just about to spawn. It is therefore suggested that the spawning-concentration of blue whiting caused a feeding-concentration of hake, which was reflected in exceptionally high catches on the new grounds explored.

Otolithen und ihre Beurteilung.

Von

W. Schnakenbeck.

Hamburg.

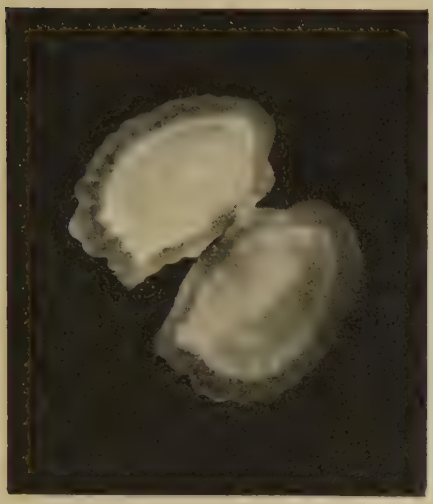
Wer sich mit der Untersuchung von Otolithen zu Altersbestimmungen beschäftigt hat, der wird die Erfahrung gemacht haben, dass sich bisweilen in dem Untersuchungsmaterial Otolithen mit zweifelhafter Deutung befanden. Schmale oder unvollkommen ausgebildete Zonen finden sich oft zwischen breiteren eingeschaltet, oder bei auffallendem Licht schwach weiss erscheinende Partien treten stellenweise in dunklen Zonen auf, und es bleibt dem durchaus subjektiven Urteil des Beobachters überlassen, in solchen Fällen zu entscheiden, ob es sich um echte »Jahres«-Ringe handelt, oder um Einschaltungen, die vielleicht durch irgend welche Unterbrechungen und durch späteres neues Einsetzen des Wachstums hervorgerufen sind. Eine wirklich sichere Entscheidung ist in solchen zweifelhaften Fällen kaum jemals möglich.

Derartige Unregelmässigkeiten und Unklarheiten treten bei den einzelnen Fischarten in ganz verschieden starkem Masse auf, und zum Teil hängt damit auch eine geringere Brauchbarkeit der Otolithen zu Altersbestimmungen bei manchen Fischen zusammen. So habe ich bereits früher bei Untersuchungen von Otolithen der Flunder (*Pleuronectes flesus*) manche Unklarheiten in der Zonenbildung feststellen müssen, die berechtigte Zweifel an der Zuverlässigkeit der daraus gezogenen Deutungen aufkommen lassen.

Nun ist mir kürzlich, ebenfalls bei *Pleuronectes flesus*, ein Fall vorgekommen, der einen unmittelbaren Nachweis der Fehlerhaftigkeit der Deutung ermöglicht.

Am 2. Oktober 1927 wurde in der Elbmündung eine Flunder gefangen, die am 5. November 1924 im Hamburger Hafen erbeutet, ge-

zeichnet und wieder ausgesetzt war. Der Fisch, ein Männchen, hatte bei der Aussetzung eine Länge von 17 cm, beim Wiederfang eine Länge von 23 cm, ist also in drei Jahren 6 cm gewachsen. Die Otolithen dieses Fisches sind in der beigegebenen Abbildung dargestellt (photographiert mit auffallendem Licht). Wenn man die sehr schmale helle Randzone als den im letzten Lebensjahre (also 1927) gebildeten Sommerring ansieht, und das muss man wohl, so wäre der Fisch im 4. Lebensjahr oder, anders ausgedrückt, 3 volle Jahre alt (also III-Gruppe). Er müsste also Anfang — sagen wir Februar — 1924 geboren sein. Zur Zeit seines ersten Fanges und der Markierung (5. Nov. 1924) wäre er also noch nicht ein Jahr alt gewesen, hätte also der 0-Gruppe angehört. Nun mass aber der Fisch damals (5. Nov. 1924) 17 cm. Und eine Flunder der 0-Gruppe kann niemals schon so gross sein, selbst nicht in der Elbe, in der das Flundernwachstum ziemlich gut ist. Ein durchschnittlicher Jahreszuwachs von 2 cm in den letzten drei Jahren deutet im übrigen auch nicht darauf hin, dass dieser Fisch konstitutionell besonders schnellwüchsig gewesen wäre.



Aber es lassen sich auch andere Belege dafür anführen, dass der fragliche Fisch im November 1924 nicht der 0-Gruppe hat angehören können. An den gezeichneten Flundern wurden nach ihrer Einlieferung Altersuntersuchungen vorgenommen. Von den kurz nach der Aussetzung, im November und Dezember, wiedergefangenen Fischen gehörte nicht ein einziger der 0-Gruppe an, die durchschnittliche Länge der I-Gruppe betrug aber 18,3 cm (bei diesem Durchschnittswert sind als Korrektiv für die Abrundung nach unten auf ganze Zentimeter beim Messen bereits 0,5 cm hinzugerechnet). Aus anderen früheren Altersuntersuchungen ist als durchschnittliche Länge der Elbflundern der 0-Gruppe im November 7,5 bis 8,5 cm gefunden, wobei die Maximalgrösse 13 cm (bei 2 Exemplaren unter 315 Angehörigen der 0-Gruppe) betrug.

Nun wird man einwenden können, dass ein Irrtum in der Messung oder ein Schreibfehler vorliege: Das ist aber höchst unwahrscheinlich.

Ein Butt von 17 cm ist eine der geringsten Längen, die von uns zur Markierung verwandt werden und überhaupt verwandt werden können; denn die in Deutschland gebräuchlichen Hartgummimarken mit der ziemlich umfangreichen konischen Spitze und dem dicken Stiel lassen die Verwendung bei kleineren Fischen nicht zu, weil die Marken zu leicht ausreissen würden. An der Richtigkeit der Grössenangabe ist also nicht zu zweifeln.

Es ist mit der Veröffentlichung dieses besonderen Falles nun nicht etwa beabsichtigt, an Hand dieses einen Beispieles die Grundlagen für die Methodik der Altersuntersuchungen mit Hülfe der Otolithen, d. h. die Deutung der Ringe als Wachstumszonen, zu erschüttern. Dieses Beispiel soll lediglich zeigen, dass die Zonenbildung nicht immer so ganz klar ist, dass selbst dann, wenn die Deutung ganz einwandfrei zu sein scheint, sie nicht immer unbedingt einwandfrei ist. In vielen Fällen wird ein kritischer Beobachter selbst zu dem Urteil »unklar« kommen. Bei dem hier erläuterten Beispiel wird ein unbefangener Beobachter nie auf den Gedanken kommen, von »unklar« zu sprechen. Ich habe verschiedenen Herren, die mit der Untersuchung von Otolithen vertraut sind, ohne vorherige Erklärung der Besonderheit des Falles diese Otolithen vorgelegt, keiner hat auch nur im geringsten gezögert, die gleiche Deutung zu geben, wie ich sie selbst herausgefunden habe.

Jetzt aber, wo man weiss, dass diese Deutung nicht richtig sein kann, würde man bei genauerer Untersuchung natürlich noch etwas Anderes herauslesen können (in anderen Fällen würde mancher »hineinrätseln« sagen). So kann man zwischen dem 2. und 3. Sommerring (Kern mitgerechnet) eine ganz schmale, nicht einmal vollkommen geschlossene, fast schemenhaft zu nennende helle Zone bemerken. Da wir in diesem Falle wissen, dass der betreffende Fisch mindestens ein Jahr älter sein muss, als er nach unbefangener Prüfung der Otolithen zu sein scheint, so ist es möglich, dass es sich hier um eine schwach ausgebildete Jahreszone handelt.

Aber wo und wie wollen wir in den vielen tausend anderen Fällen, in denen eine Nachprüfung wie hier nicht möglich ist, entscheiden, ob es sich bei solchen schemenhaften, unvollkommen ausgebildeten Ringen um wirkliche Jahreszonen handelt? Es sind doch auch so viele andere Fälle denkbar, bei denen Wachstumsunterbrechungen vorkommen können, seien sie durch Ernährung, Temperatur, Krankheit oder andere äussere oder innere Anlässe hervorgerufen; wir wissen ja nicht, welches die eigentliche Ursache, das physiologische Agens dieser Zonenbildung ist. Gewissermassen aufgeteilte Ringe, Einschaltung ganz schwacher Ringe, Auftreten unvollkommener Ringe und viele andere mannigfach

variierende Vorkommnisse finden sich bei den Otolithen in überaus zahlreichen Fällen. Wo ist da die Grenze zwischen Unregelmässigkeiten in der Anlage innerhalb einer Jahreszone und Hemmungen in der Ausbildung einer ganzen Jahreszone.

Der erläuterte Fall zeigt, dass Irrtümer in der Deutung der Otolithenzonen vielleicht häufiger sind, als wir ahnen. Ganz vermeiden lassen sich diese Fehler nicht, sie lassen sich nur abschwächen durch die Verwendung sehr umfangreichen Materials.

A Transparent Bucket with a detachable bottom for use with Ostenfeld and Jespersen's Standard Net for Plankton Collection.

By

R. S. Wimpenny, M. Sc.
Fisheries Laboratory, Lowestoft.

For the sake of uniformity and the mutual comparability of plankton net catches, the Plankton Committee of the International Council for the Exploration of the Sea at its meeting in October 1923 passed the following resolution: —

"It is recommended that the description of the standard net mentioned in the recommendations from 1921—1922 be published this year by the Bureau (cf. Rep. 1921 para. 1 and 1922 para. 2)." (1)

In the following August the specifications of such a net were published by Ostenfeld and Jespersen (2). The net described by these planktologists was recommended for vertical and horizontal use and has been utilised for the English plankton investigations since 1924.

While it has given every satisfaction as a vertical net, its use horizontally has suggested certain modifications. When the net is fishing horizontally near the surface and fitted in the way specified, it is noticed invariably that the terminal part of the net and the bucket bend downwards so as to be almost at right angles. The result of this bending is to constrict the end of the net and so reduce the filtering area and alter the fishing power. It was found impossible to avoid this at any speeds at which it was prudent to tow the nets. Adjustment of the bridles along the side of the net was also unsuccessful. The causes of this effect appear to be dual.

(1) The presence of the 3 lines running from the mouth of the net and ending in a stout metal ring below the bucket.
(2) The weight and construction of the metal bucket.

With regard to (1) it is suggested that when not being used as a closing-net these should be removed for horizontal hauls. In the case of the metal bucket and its clamps, it is felt that its total weight of 465 gms. indicates an unnecessarily robust construction.

Advantages to be desired in a bucket used on a tow-net which frequently yields a big catch are, facilities for inspecting the catch and, when many nets are used on one line and are required again immediately, some method of taking off the catch and refitting the buckets of the

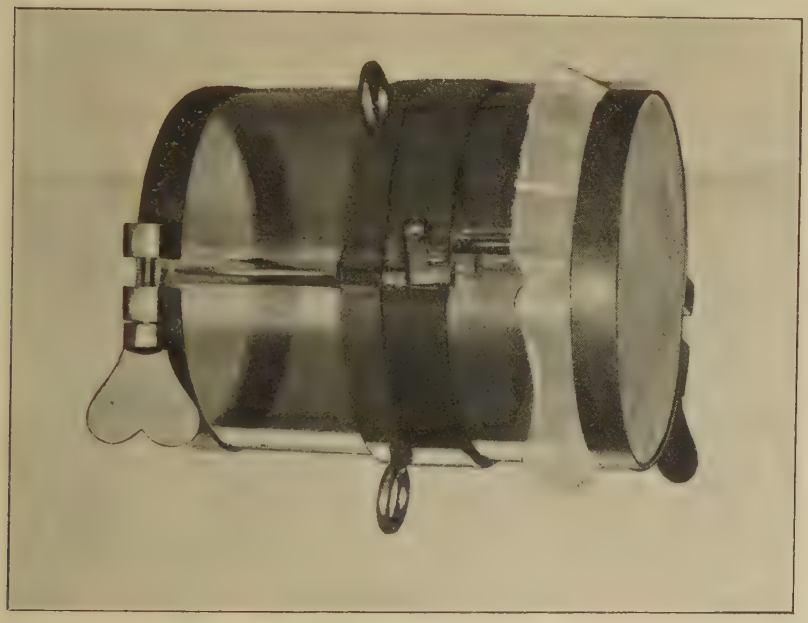


Fig. 1. Bucket with parts in position.

same nets in the least possible time. In an opaque bucket, as one cannot see the catch, great care has to be exercised in allowing the bucket to drain sufficiently, otherwise on undoing the bottom clamp, a large amount of fluid gushes out and may overflow the limits of the vessel into which it is being delivered. These operations of draining and preserving take up some time, especially if several nets are being dealt with at once, and it is desired to fish another string of nets in a deeper layer. In this case removable and interchangeable bottoms would be very desirable; for the catch from a net that has just fished may be taken off and dealt with later, whilst a spare bottom is rapidly fitted to the net and the latter is ready for use again immediately.

To fulfil these desiderata there has been made a transparent celluloid

bucket of the same dimensions as the bucket of the standard net, but with a removable bottom (figs. 1 and 2). The bucket has already been used and has proved very convenient.

A dimensional diagram is given in figure 3.

The device consists of two collars, the top one 7 cms. deep (*TH*) and the bottom one 5 cms. (*BH*). Both are made of celluloid 1 mm. thick. The bottom collar fits inside the top one, making a flush joint 1.5 cms. from the bottom edge of the top half. The top half consists of a collar of celluloid 5.5 cms. deep, having another ring of celluloid 2.5 cms. deep fixed around its base 1 cm. from the bottom of the first collar. This pro-

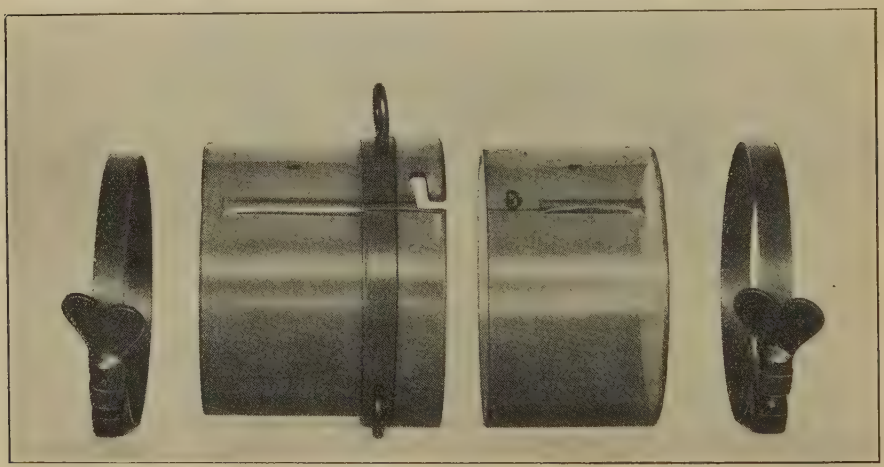


Fig. 2. Dissection of bucket.

vides 1.5 cms. of overlap into which the bottom half fits. At opposite sides of this piece of overlap there are cut two curved channels into which fit studs of brass on the outer surface of the bottom half. This forms two bayonet joints (*B.J.*) which allow the bottom half of the bucket to be pushed home and locked.

In the part of the top half forming a thickened belt owing to the two layers of celluloid, three rings 1.9 cms. in diameter are arranged at 120° to each other. They are set in the equatorial plane of the bucket rather than the longitudinal plane as in the original metal bucket. This facilitates the passage and attachment of the lines or bridles when used. They may be run easily through the rings, and attached at the point desired, or allowed to run free. The bucket is attached to the net by a thin brass clamp 9 mm. deep (*T.C.*) and tightened by a butterfly screw. A similar

clamp secures the silk over the bottom of the bucket. (B.C.) The total weight of the bucket and the clamps is 150 gms.

My thanks are due to Mr. J. O. Borley of this Laboratory for helpful suggestions and criticisms during the construction of this bucket and its precursors.

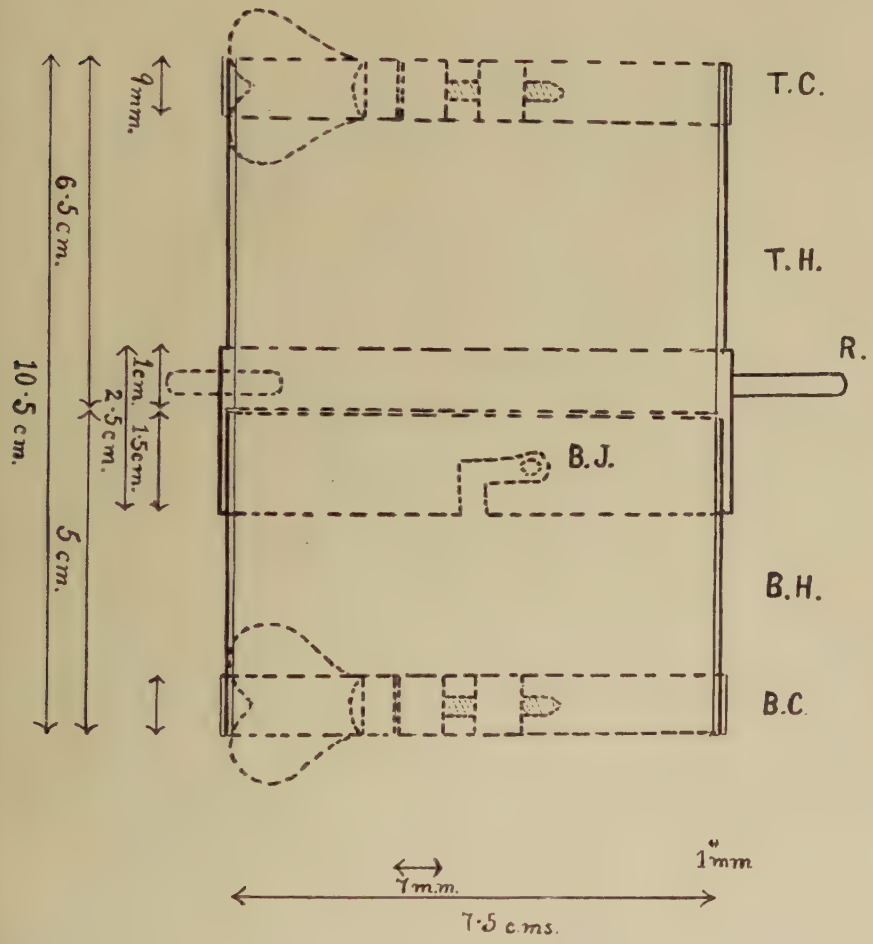


Fig. 3. Dimensional diagram of celluloid bucket. T.H. Top half. B.H. Bottom half. B.J. Bayonet joint. T.C. Top clamp. B.C. Bottom clamp. R. Ring for bridles.

References.

1. Rapports et Procès-Verbaux des Réunions. Conseil Permanent International pour l'Exploration de la Mer. (Octobre 1923.)
2. Ostenfeld, C. H., and Jespersen, P., Standard net for Plankton Collections. Publications de Circonstance No. 84. 1924.

Fluctuations in the larval Stages of Euphausiidae off Möre, 1926–1927.

By

Johan T. Ruud.

Biological Laboratory, University of Oslo.

During the continued plankton investigations off Möre in 1927, there where collected, as in the two preceding years, observations regarding Euphausiidae. The material thus collected consists partly of samples of "krill" (fry) taken from the oesophagus of whales (*Balaenoptera physalus*), and partly of a quantity of tow-net samples. A preliminary report of the material from 1925 and 1926 was given earlier[1]).

It is well known that the quantity of Euphausiidae, which play an important part in the food of whales, herring, etc., undergoes great changes from one year to another. It is our hope that in the course of time we shall be able to contribute towards the solution of this question which is of such great interest in the biology of the "krill". The existing material, however, is still of such limited scope that at present we are unable to say more regarding the adult Euphausiidae beyond what has been mentioned in the above-mentioned report as regards their occurrence and spawning.

In 1927 several circumstances resulted in the stations with tow-nets not being utilized as methodically and to the extent which might have been desirable with the investigations in view. Thus accordance between the stations during recent years has not been particularly good as regards time and place. Nevertheless the euphausiid larvae occurring appear to show conditions which we consider are worthy of mention even at the present juncture.

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[1]) Rapports et Procès-Verbaux des Réunions Vol. XLI. Sept. 1926, pp. 107—122. "Report of the Area Committees, North Eastern Area 1925—1926" by Johan Hjort and "Appendix A" by Johan T. Ruud.

Table of larval Stages of Euphausiidae in townets off Möre.

			M. norvegica	Th. inermis
1926.				
St. 58. $^{29}/_{4}$ 26 15′ NW $^{1}/_{2}$ W Ona	Townets	Surface 10′	..	243
		100 m wire 10′	..	156
		200 m wire 10′	..	375
St. 64. $^{12}/_{5}$ 26 45′ NW Björnsund	Townets	Surface 15′	1	3
		100 m wire 15′	..	1
		200 m wire 15′	..	7
St. 82. $^{25}/_{6}$ 26 45′ NW Bj.sd.	Townet	300 m wire 15′	13	2
St. 83. $^{25}/_{6}$ 26 8′ NNW Bj.sd.	Townet	200 m wire 20′	3	10
St. 84. $^{12}/_{7}$ 26 5′ NNW Bj.sd.	Townet	200 m wire 10′	3	12
St. 85. $^{20}/_{7}$ 26 Julsund	Townet	100 m wire 10′	..	16
St. 86. $^{20}{}_{7}$ 26 5′ NNW Bj.sd.	Townets	100 m wire 10′	9	217
		200 m wire 10′	14	113
St. 87. $^{20}/_{7}$ 26 17′ NW Bj.sd.	Townet	100 m wire 10′	17	31
St. 88. $^{20}/_{7}$ 26 32′ NW Bj.sd.	Townet	75 m wire 10′	13	18
St. 90. $^{21}/_{7}$ 26 43′ NW Bj.sd.	Townets	50 m wire 30′	27	7
		150 m wire 30′	21	9
		300 m wire 30′	11	6
St. 92. $^{21}/_{7}$ 26 10′ NW Bj.sd.	Townet	150 m wire 10′	16	36
St. 92. $^{21}/_{7}$ 26 8′ NW Ona	Townets	50 m wire 30′	31	74
		150 m wire 30′	14	19
		250 m wire 30′	78	12
1927.				
S/S Östkap st. 1. $^{20}/_{5}$ 27 NW St. hest. 35′	Townet	Surf. 3′	50	3
St. 120. $^{21}/_{5}$ 27 9′ NW Ona	Townets	Surface 20′	18	..
		100 m wire 20′	330	114
		300 m wire 20′	1116	180
S/S Östkap st. 2. $^{23}/_{5}$ 27 poss.?	Townet	Surface 10′	117	61
St. 125. $^{1}/_{6}$ 27 48′ NW Bj.sd.	Townet	50 m wire 20′	59	17
S/S Östkap st. 3. 48′ NtW Bj.sd.	Townet	100 m wire 2 h.	37	18
S/S Skagerak st. 139. 75′ NW Bj.sd. $^{1}/_{8}$ 27		100 m d. 10′	6	15
S/S Skagerak st. 143. 210′ NW Bj.sd. $^{2}/_{8}$ 27		10 m 20′	1	87
		20 m 20′	168	384
		60 m 20′	37	109
		100 m 20′	34	70
		200 m	3	27

In the above table the figures for Euphausiidae were found by simple counting (in very large samples by counting the aliquot parts). Discrimination has been made between *Meganyctiphanes norvegica* and *Thysanoessa inermis*. In the case of the latter there is the reservation that other Thysanoessa species are also included in the counting, since the

MØRE 1926-27.

separation into species in the most minute stages is arduous, and in addition they appear to be in the minority. Moreover in the figures all the stages from Calyptopis to the last Cyrtopia inclusive are combined.

By comparing the table with the above sketch map it is seen that the stations which are situated above the deep channels in the bank and in the vicinity of the shelf are richest in euphausiid larvae. This agrees with our previous observations of spawning at those places.

The larvae, however, are far more dependent upon conditions of current than are the adults, and we therefore find them over the entire bank and in the fjord.

In this connection it may be mentioned that in most of the samples of both years there were not a few furcilia and cyrtopia stages of *Nyctiphanes couchii* which is not found to be adult or spawning in our waters.

In 1926 the Stations with townets were represented during the period $^{17}/_{3}$ to $^{21}/_{7}$ inclusively. Euphausiid larvae do not appear in appreciable numbers until $^{28}/_{4}$. We then have also the maximum of *Th. inermis*, viz. 375, with 200 m. w. at Station 58, whilst at the same place spawning

of the same species was found on $^{17}/_{3}$. *Th. inermis* has since been well represented throughout the season, but *M. norvegica* does not occur in appreciable quantities until $^{25}/_{6}$ on the shelf, where we found spawning of *Meganyctiphanes* at the beginning of May. The maximum number of larvae of this species was not observed until the $^{21}/_{7}$, viz. 78 specimens.

In 1927 there have been a number of good townet hauls during the period $^{20}/_{5}$ to $^{1}/_{6}$, and one station on $^{1}/_{7}$. These hauls show a relatively large number of *Meganyctiphanes norvegica*, the maximum being 1116 specimens at Station 120, 300 m. w. 20′ whilst the corresponding figure for *Th. inermis* is 180. This mass appearance of *M. norvegica* at such an early stage may perhaps indicate that spawning took place earlier in 1927 than in 1926. This cannot be definitely concluded since on account of fewer cruises we missed the spawning in 1927. On the other hand we have no satisfactory townet figures from the period $^{12}/_{5}$—$^{25}/_{6}$ 1926, so that we cannot with certainty decide whether similar conditions were present in 1926 or not.

Stations 139 and 143 occupy a special position in 1927 on account of their situation outside the Gulf Stream. The high values of *Th. inermis* are here misleading since the more oceanic form *Th. longicaudata* is very common in these samples.

The figures which are to be found in the table may appear to be small, but this is due to the fact that the towings are of relatively short duration. This again is due to the circumstance that hauls of longer duration with such fine nets as are necessary for the larvae, are rendered impossible by the large quantities of copepodae which are to be found at that time.

The small figures in connection with the unsatisfactory agreement between the stations during the two years exclude extensive conclusions as to the material to hand. We believe, however, that we are entitled to assume, that the two years 1926 and 1927 were different in this respect, that in 1926 the dominating species was *Th. inermis*, while in 1927 larvae of *M. norvegica* were in much greater abundance. - This also appears to be shown by the vertical hauls, even though the material may be inadequate for a complete treatment.

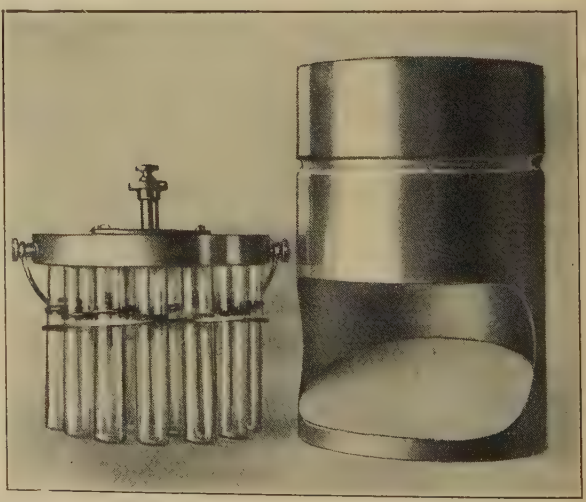
A new Colour Comparator.

By

Oscar Sund, Bergen.

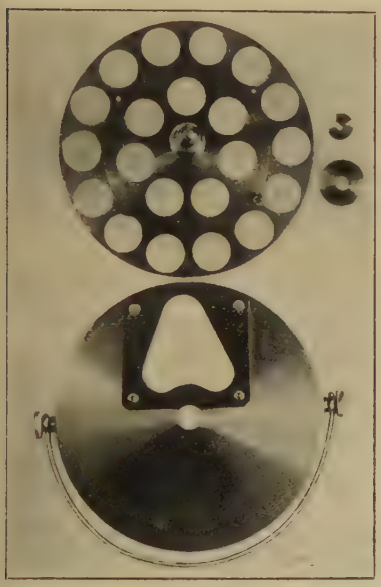
The usual implement for comparing colorimetric samples is a long rack with holes for a number of glass tubes, every other place being occupied by the tubes containing the standard solutions. Now this long rack is very bulky and entails the use of some other stand to receive the samples not actually under comparison, and to find the right interval one has to try the sample tube in different positions. This means some unnecessary loss of time, and time as well as space is generally scarce at sea.

In order to save both to some extent I have had made the simple contrivance illustrated here. It consists essentially of a brass box (12 × 18 cm.) the under part of which has a large opening to admit the light which is reflected upwards from an inclined pane of milk glass. The glass tubes used are the common flatbottomed type 15 × 100 mm. Each of them is provided with a rubber string band which is so placed that there will be room for 10 ccm. below (or another desired quantity). The glass tubes are placed in the holes of the plate, hanging on the rubber bands. The plate consists of two parts which can be moved by turning the head of the stem which comes up through the lid. If the head is slightly



pressed down at the same time, only the inner portion, carrying the standards moves, if it is slightly raised, both parts will move.

The lid is secured to the box by two screws which also serve as supports for the handle (this for convenient stowing away when not in use).



The hole in the lid will admit of the inspection of two standards and one sample (or two samples if the plate with the triangular hole is removed). One has first to bring the sample in position by turning the head and lifting it slightly, and then bring the proper two standards into position when pressing the head. The outer ring carrying the samples will then remain in position because the ring presses against its conical support at the edge. The holes are distinguished by numerals embossed in convenient positions. In the example used on board the "Johan Hjort" for p_H determinations, the seven inner holes are numbered 3 to 9 to correspond directly to the numbers of the standard borax-boric acid solutions employed, the outer row of 14 holes 1 to 14 corresponding to the numbers of the reversing water bottles in use. A duplicate, for comparing samples mixed with the Harvey nitrate reagent, has the same numbering on the outer ring, but 1 to 7 on the inner. (It has been found that this way of comparing the nitrate samples is superior in more than one respect to the use of a colorimeter, and much quicker).

It is as a rule not necessary to remove the lid when the apparatus is to be used. The tubes to receive the samples are picked out and filled from the water bottles one by one through the hole in the lid. A clean rubber stopper, kept for the purpose in a small glass bottle, should be used when mixing the sample with the indicator. When all the samples are put in their respective places, the stoppers closing the standard tubes are removed and these will remain uncovered only the very few minutes required for inspecting the samples.

The Comparator is made by the firm Bergen Nautik, Bergen.

Note on the Theoretical Courses of Ocean-Currents.

By

V. Walfrid Ekman, Lund.

In a paper[1]) of 1923 I deduced dynamically some mathematical equations showing a close dependence of a current on the topography of the sea-bottom and the direction of the North. Particularly the investigation had for its object the laws governing the currents produced by gravity in homogeneous water when the sea-surface is inclined to the horizon. Such currents, when running from a deeper towards a shallower part of the sea or *vice versa*, were proved to be subject to a "topographic rotational effect" causing them to deviate cum sole or contra solem respectively (i. e. to the right or to the left in northern latitudes). Likewise a current not moving due east or west would be subject to a "planetary rotational effect" causing it in most cases to deviate eastwards. The two effects combined would govern the actual course of the current.

Now this simple theory appears to need improvement on an important point; and since its results have actually been referred to for the interpretation of oceanographical observations, I think it would be proper at an early convenience to point out its principal defect and the directions in which its results are likely to be modified. I am indebted to the Editor, who has at rather short notice kindly found room for this note. It is hoped that a fuller account of the subject will appear within not too long a time in another place.

The original simple theory was founded on the assumption that the real forces acting horizontally on a mass of water are sufficiently accurately balanced by the Coriolean force due to the earth's rotation, so that the acceleration of the water relative to the earth can be left

[1]) "Über Horizontalzirkulation bei winderzeugten Meeresströmungen", Arkiv f. Mat. Astr. o. Fys. 17 Nr. 26, Stockholm 1923.

See also the article "Meeresströmungen" in "Handbuch der physikalischen und technischen Mechanik" herausg. von F. Auerbach und W. Hort, B. 5, Leipzig 1927.

out of account in the dynamical equations. In a previous paper[1]) I have given reasons for this assumption, and no doubt it is for most purposes legitimate, when actual stationary ocean-currents are being considered. However, in the theory in question even a very minute acceleration will be of importance, if the depth of the sea is many times greater than the "depth of frictional influence". For this particular purpose therefore, the assumption is not legitimate.

The principal alterations to be made are best explained by the help of the following two simplified equations representing the original and the revised theory respectively. In both equations terms which, though not insignificant, are of an inferior order of importance have been omitted. The equations are in the case of the original theory:

$$\frac{D''}{2\pi d} \cdot \frac{1}{G} \operatorname{curl} G = \frac{1}{d} \frac{\delta d}{\delta s} - \frac{\cos \alpha}{R \tan \varphi} \tag{1}$$

and in the case of the revised theory:

$$\frac{D''}{2\pi d} \cdot \frac{1}{G} \operatorname{curl} G + \frac{1}{2\omega \sin \varphi} \frac{\delta \operatorname{curl} G}{\delta s} = \frac{1}{d} \frac{\delta d}{\delta s} - \frac{\cos \alpha}{R \tan \varphi}. \tag{2}$$

Here d is the depth of the sea and D'' is the "bottom" value of the "depth of frictional influence", so that at all levels at a greater distance than D'' above the sea-bottom, the current has — in any case within the homogeneous deep water — one direction and velocity; this direction and velocity being denoted by the letter G. R is the earth's radius, ω its angular velocity and φ the latitude; and α is the angle between the meridian (drawn towards increasing latitudes) and the direction of the current G. Finally curl G is the well-known vector operation of G equal to twice the average velocity of rotation of the water, this rotation being reckoned positive when running contra solem: and $\delta/\delta s$ means a derivative taken along the course of the current itself, so that for instance $\delta d/\delta s$ is the slope of the sea-bottom in the direction of the current.

The interest attached to these equations is chiefly due to the circumstance that they might give values of curl G greater than would be consistent with any current of a not altogether local character. Currents carrying water from one part of the ocean to another must follow such courses that this does not happen.

It is difficult at present to say anything for certain about the relative

[1]) "Beiträge zur Theorie der Meeresströmungen", Ann. d. Hydrographie u. marit. Meteorologie, 34, 1906.

magnitude and importance of the two terms on the left hand side of equation (2), since it partly depends on the velocity of the current and other circumstances which are still unknown or varying from one part of the ocean to another. The new, second term may under certain circumstances be of inferior importance, but in other cases it might be the dominating one.

The first term on the right hand side represents the topographic rotational effect. According to both theories this effect leaves the current unaffected only in the case when the latter is following the level lines of the sea-bottom; and it very effectively prevents the current (by deviating it to the right or to the left) from traversing a bottom ridge or groove or from entering into a deeper or a shallower part of the sea, if the differences of depth are large enough.

The important alterations are the following:

Firstly. According to the original theory (equation 1) the curvature of the stream-lines is directly connected with the slope $\delta d/\delta s$ of the sea-bottom, the current turning contra solem when running in the direction of deeper water and cum sole when running in the direction of shallower water. According to the revised theory the connection is a more complex one, so that there is a tendency to contra solem rotation not only where the water is deepening in the direction of the current but also where the depth is a maximum, and vice versa.

Secondly. According to the original theory the power of a submarine ridge (or groove) to prevent a current from traversing it would depend simply on its absolute height as compared to D''. According to the revised theory this power will depend on various circumstances. A certain height as compared to D'' will always be necessary for the purpose, but the depth of the sea and the velocity of the current are of consequence as well. For even if the height of the ridge (or the depth of the groove) exceeds D'', it will not effectively check the current, if the area of its cross-section is sufficiently small as compared to the area swept out by a drifting plumb-line reaching from the surface down to the bottom and drifting with the current for one pendulum day (24 sidereal hours divided by sin φ).

As far as the planetary effect alone is concerned (represented by the second term on the right hand side) the results of the theory seem to be in the main unaltered, the directions of currents being still in low latitudes restricted to east or west approximately.

Finally I wish to emphasize the observation in my 1923-paper that the above-mentioned laws refer only to the gradient currents in homogeneous water and to some extent to convection currents carried along

on top of such gradient currents. They do not refer to convection currents in the upper layers in cases where the deeper water-layers have no appreciable motion. As to the apparent connection between the bottom-topography and the various bends in the paths of ocean-currents which may be observed on oceanographical maps, its dynamical explanation does not seem to be quite clear yet, and I would not like to enter upon this matter for the present.

Reviews.

Neue Dänische Untersuchungen über die Brut der Plattfische und die »Fluktuationen« derselben.

Von A. Bückmann, Helgoland.

Ein ganz besonderer Nachdruck ist in letzter Zeit auf die Erforschung der sog. natürlichen Schwankungen («Fluktuationen») der Bruterzeugung auch bei Plattfischen (vornehmlich der Scholle) gelegt worden. Es liegen gegenwärtig vier Arbeiten vor, die diese Frage zum wichtigsten Gegenstande haben und sich mit den dänischen Gewässern vom Limfjord und dem Skagerrack bis zur Beltsee und mit der eigentlichen Ostsee (Baltic Proper) beschäftigen. Es sind dies:

1) Blegvad, H., On the Renewal of the Stock of Plaice in the Baltic Proper, in: Rep. Dan. Biol. Stat. XXXII, 1926 (Kopenhagen 1927).
2) Blegvad, H., On the Annual Fluctuations in the Age Composition of the Stock of Plaice, und
3) Johansen, A. C., On the Fluctuations in the Quantity of Young Fry among Plaice and certain other Species of Fishes, and Causes of the same, beide in: Rep. Dan. Biol. Stat. XXXIII, 1927 (Kopenhagen 1927).
4) Bruun, A. Fr., Quantitative Investigations of the 0-Group and I-Group of the Plaice, Turbut, Brill, and Sole in the Skagerrak, Kattegat and Belt Sea. Meddelelser fra Komm. f. Havunders. Ser. Fisk. Bd. VIII. Nr. 5.

Die an vierter Stelle genannte Arbeit ist dem Zeitpunkt ihrer Erscheinung nach zwischen 1) und 2) zu stellen. Die vier Werke haben ein so gemeinsames Gebiet und unter einander so grosse Bedeutung für die Beurteilung der gesamten Ergebnisse, dass sie am besten gemeinsam besprochen werden.

1) Die erste der Blegvad'schen Arbeiten behandelt ein viel umstrittenes Gebiet. Bekanntlich waren bei den ersten Untersuchungen, die an den Küsten der eigentlichen Ostsee angestellt wurden, so wenig Schollen des ersten Lebensjahres angetroffen worden, dass Petersen zu der Anschauung kam, dass der Bestand von aussen her — durch Einwanderung aus Kattegat und Beltsee — Nachwuchs erhielte. 1907 aber fand Johansen sowohl pelagische Brut als auch Bodenstadien der 0-Gruppe in grösserer Menge, letztere jedoch nicht wie in anderen Gebieten an der Küste, sondern in tieferem Wasser (über 10 m).

Blegvad hat nun bei den im Jahre 1925 von der Dänischen Biologischen Anstalt in der eigentlichen Ostsee ausgeführten Arbeiten die ersten Bodenstadien der Scholle in namhafter Menge im ganz flachen Was-

ser gefunden. Die Untersuchungen wurden an den Küsten von Bornholm, Seeland, Möen und Falster vornehmlich mit dem Schiebehamen ausgeführt. Die grössten Fänge (bis 59 Stück in $^1/_2$-stündigen Hamenfängen) wurden auf Seeland und Falster gemacht; der Autor vermeidet es jedoch — und sehr mit Recht -Mittelwerte aus der im Verhältnis zur Küstenstrecke immerhin noch geringen Zahl der Untersuchungen zu ziehen. Auch in tieferem Wasser wurden Bodenstadien in grösserer Menge an gewissen Stationen gefangen. Gearbeitet wurde hier mit einem engmaschigen Scherbrettnetz und dem Jungfischtrawl, stets mit beschwertem Grundtau. So sind leider die hier gefangenen Mengen mit denen von der Küste nur zu einem sehr geringen Teil direkt vergleichbar. Die grössten 0-Gruppenfänge wurden querab Darsserort gemacht, und leider fehlen gerade hier deutsche Küstenuntersuchungen im Jahre 1925. (S. Wiss. Meeresuntersuchungen, Abt. Kiel, Bd. XX.). Der Verfasser ist der Ansicht, dass die Schollen der 0-Gruppe von der Küste her in das tiefere Gebiet eingewandert sind. Dafür spricht entschieden, dass die in der Tiefe gefangenen im Mittel grösser sind als die aus der Küstenzone, (nicht, wie Johansen aus seinem in dieser Beziehung unvollkommeneren Material glaubte schliessen zu müssen, kleiner), und dass sie nur an bestimmten, von der Küste her sich flach abdachenden sandigen Stellen der tieferen Region vorkommen, später im Jahre in grösserer Zahl als anfangs.

Die Ursache, weshalb in früheren Jahren niemals reichlich Jahresbrut an den Küsten der eigentlichen Ostsee gefangen wurde, sieht der Verfasser einerseits in der Unzulänglichkeit der Untersuchungen in einzelnen Jahren, andererseits aber darin, dass die Jungschollenproduktion der einzelnen Jahrgänge in hohem Masse schwankt und hier, nahe der Grenze des Artvorkommens, in extrem ungünstigen Jahren fast gänzlich gleich 0 werden kann. Auf Grund der Untersuchungen von 1923 bis 1925 (später ergänzt durch die von 1926) über die Jahresbrut bzw. die Häufigkeit der älteren Jahrgänge im Bestande kann der Verfasser nachweisen, dass ausser dem Jahrgang 1925 noch die Jahrgänge 1923 und 1921 reichlich, 1922 dagegen und vor allem 1924 spärlich vorhanden sind.

Als Ursache für die Jahresschwankungen ergeben sich die wechselnden hydrographischen Verhältnisse des Gebietes. Hohe Temperatur und hoher Salzgehalt in den tieferen Wasserschichten der Ostsee während der ersten Monate des Jahres begünstigen die Entwicklung der Schollenbrut, während umgekehrt geringer Salzgehalt und niedrige Temperatur ungünstig sind. Um das festzustellen, werden nicht Monatsmittel der hydrographischen Daten gegeben, die nach Ansicht des Verfassers leicht irreführen können, sondern eine allgemeine Charakteristik des Zustandes.

Nach der Ueberzeugung des Referenten ist der Nachweis, dass die Schollen der 0-Gruppe in der Ostsee sich wie in anderen Meeresteilen zunächst in der flachen Küstenzone aufhalten und von dort aus in die Tiefe wandern, äusserst wertvoll. Es bedarf aber zweifellos noch jahrelang fortgesetzter Untersuchungen, um festzustellen, ob das in allen Jahren in derselben Weise der Fall ist. Ref. hält es für wesentlich zu erwähnen, dass — nach den bisherigen Helgoländer Untersuchungen zu urteilen — Schollen der 0-Gruppe im Sommer in der Nordsee in tieferem Wasser nicht

entfernt in so grosser Zahl gefangen werden können, wie JOHANSEN und der Verf. gefunden haben.

2) Die Frage der Schwankungen in der Jungfischerzeugung behandelt BLEGVAD in seiner zweiten Arbeit für die Beltsee, den Sund, das nördliche Kattegat und verschiedene Teile des Limfjords. Er gründet seine Schlüsse auf die Veränderung der Alterszusammensetzung des Bestandes in mehreren aufeinanderfolgenden Jahren, 1923—26. Die Fänge sind vorwiegend mit einer Aalzeese mit Scherbrettern gemacht, und das Material aus diesen Fängen ist ergänzt durch Untersuchung von Fängen praktischer Fischer. Fassen wir die Angaben über den Ausfall der Jahresbruten in den untersuchten Gebieten, ergänzt durch die vorerwähnten aus der eigentlichen Ostsee zusammen und bezeichnen gute Jahrgänge durch ein +, schlechte durch ein —, so ergibt sich folgendes Bild:

	1920	1921	1922	1923	1924	1925
Eigentl. Ostsee	.	+	—	+	—	+
Beltsee	.	+	—	+	—	+
Nördl. Kattegat	.	.	.	.	—	+
Limfjord	+	—	+	+	—	+

Unterstützt werden die Angaben für die Beltsee durch Dichtebestimmungen an der I-Gruppe, während sie für Kattegat und Limfjord aus dem relativen Verhalten der Altersklassen allein erschlossen werden. Im Sund scheint der Bestand — nur ältere Schollen — aus der Ostsee her einzuwandern. Im nördlichen Kattegat sind die Jahrgänge in ihrer relativen Stärke nach dem Befunde des Autors beiweitem nicht in dem Masse verschieden wie in der Beltsee, nur 1924 markiert sich als schlechter, 1925 als guter Jahrgang. In Belt- und Ostsee sind die Verhältnisse, soweit man sieht, vollständig die gleichen. Deutlich abweichend verhält sich der Limfjordbestand, der sich aus der Nordsee rekrutiert. Es scheint dem Ref. bemerkenswert, dass der in der südlichen Nordsee so schwache Jahrgang 1923 hier reichlich in Erscheinung tritt (obwohl entschieden nicht in dem Masse wie der von 1922), während im Uebrigen deutliche Uebereinstimmung mit den in der Nordsee beobachteten Verhältnissen festzustellen ist.

Aus den Limfjorduntersuchungen ergeben sich interessante Einzelheiten über die Wanderungen der Schollen zwischen den inneren und äusseren Teilen des Fjords. Interessant sind auch die Betrachtungen des Autors über die Auswirkungen des wechselnden Ausfalls der Jahresbrut für die Fischerei in der Beltsee.

3) JOHANSEN geht näher auf die Ursachen der Fluktuationen ein. Er gibt eine Aufzählung der Möglichkeiten, die zu dem verschiedenartigen Ausfall der Jahresbruten führen können und führt für einige derselben Beispiele an. Die wichtigste Ursache sieht man allgemein in der Gunst oder Ungunst der Bedingungen für das Aufwachsen der Brut, vor allem der hydrographischen Verhältnisse. Die Untersuchungen der Dänischen Kommission für Meeresforschung über die Menge der jungen Schollen der 0- und I-Gruppe im Küstengebiet der Beltsee einschliesslich des südlichen Kattegats, ausgeführt mit dem Dänischen Jungfischtrawl nach JOHANSEN, bilden das Material, mit dem er arbeitet. Auf Grund der so gewonnenen

Zahlen erscheint übrigens das Jahr 1921 als ungünstig für die Jungfischerzeugung, während es sich nach den Bleegvad'schen Untersuchungen als günstig darstellt. Darauf wird noch weiter unten einzugehen sein. Interessant ist die Methode, wie die Werte der Jungschollendichtigkeit berechnet werden. Einmal wird die Fangmenge an 0-Gruppe pro Fangstunde berücksichtigt, dann soll aber auch der Fang an I-Gruppe im nächsten Jahre für die Wertung des betr. Jahrgangs in gleichem Masse in Rechnung gestellt werden. Da aber in den Fängen des Jungfischtrawls in diesem Gebiet dreimal soviel 0-Gruppe wie I-Gruppe enthalten ist, werden die Werte der I-Gruppe vor der Vereinigung mit denen der 0-Gruppe auf das Dreifache erhöht. Dies Verfahren wird nach Ansicht des Referenten wohl nur dann zweckmässig sein, wenn der Fang des Netzes für die I-Gruppe in gleichem Masse repräsentativ ist wie für die 0-Gruppe, was dem Referenten nach den bisherigen deutschen Untersuchungen nicht ganz sicher erscheint. – Nun wird die Dichtigkeit der Schollenjahrgänge verglichen mit den Salzgehalts- und Temperaturanomalien des Oberflächenwassers beim Feuerschiff Schultz' Grund. Der Augenschein lehrt, dass Jahre mit positiver Abweichung von Temperatur und Salinität in den ersten drei Monaten des Jahres mit reichen Brutjahrgängen zusammenfallen. Die Errechnung des Korrelationskoeffizienten für die einzelnen Monate und für alle drei zusammen kann den Eindruck kaum noch verstärken, doch scheint es, als ob die Salinität der ersten beiden Monate ausschlaggebender sei als die des März. Auch die Zahl der Eistage in den einzelnen Jahren wird mit der Jungschollenmenge verglichen. Hier zeigt sich ebenfalls eine gewisse Uebereinstimmung.

Es wird nun die Frage diskutiert, wie die Wirkung der hydrographischen Faktoren zu erklären ist. Im Untersuchungsgebiet kommt direkte Einwirkung nur in geringem Masse in Frage, da tötliche Minima im allgemeinen nicht oder nur an einzelnen Stellen erreicht werden. Die Wirkung wird als indirekte angesehen, die Beeinflussung der Nahrungsmenge wird für das Wahrscheinlichste gehalten. Das wird nachgewiesen an dem Zusammenhang zwischen dem Salzgehalt und der Menge des Planktons nach Untersuchungen aus den Jahren 1906—08, sowie zwischen dem Planktonvolumen und der Jungfischmenge in den gleichen Jahren. Das Plankton haben wir ja als die Hauptnahrungsquelle der pelagischen Larven anzusehen. In diesem Zusammenhange scheint es dem Referenten überraschend, dass der Korrelationskoeffizient der Brutmenge zur Salinität im März so bedeutend kleiner ist als in den beiden ersten Monaten, da doch im März die gesamte Menge der erzeugten Larven auf Planktonnahrung angewiesen ist, während in den früheren Monaten ein Teil noch im Embryonalleben war und ein Teil der Eier noch garnicht abgelegt. Doch soll deswegen keineswegs in Zweifel gezogen werden, dass die wichtigste Ursache für den Ausfall der Jahrgänge in der Beltsee die Menge der vorhandenen Nahrung ist. Man darf wohl dem mathematischen Ergebnis keine zu hohe Bedeutung zumessen. Von grossem Interesse muss es daher nach der Ansicht des Ref. sein, dies Problem noch in den Einzelheiten zu erforschen, insonderheit womöglich festzustellen, welche Planktonarten und -Gruppen von ausschlaggebender Bedeutung sind, sodass bei geringem oder etwa ver-

spätetem Auftreten ein so grosser Teil der Larven dem Hungertode verfällt.

4) Das gesamte, seit 1905 von der Dänischen Kommission in den Gebieten vom Skagerrack bis zur Beltsee gesammelte Material an Jungfischtrawlfängen liegt auch der Arbeit von Bruun zugrunde. Er nimmt als Teilgebiete für seine Bearbeitung das Skagerrack, das nördliche Kattegat, das südliche Kattegat, die Beltsee und die eigentliche Ostsee. Aus den Gesamtzahlen der seit 1905 gefangenen Schollen errechnet er zunächst den mittleren Stundenfang an 0-Gruppe wie an I-Gruppe in jedem der Gebiete, sowie das Verhältnis zwischen beiden Gruppen. Der grösste Fang an 0-Gruppe liegt im Skagerrack, danach kommt das nördliche Kattegat. Die anderen Gebiete fallen dagegen stark ab. Jedoch wird von der I-Gruppe beiweitem am meisten im Nordkattegat gefangen, mehr als halb soviel Individuen pro Stunde wie 0-Gruppe, wogegen der Skagerrackfang ausserordentlich gering (nur ein Zehntel des Betrages der dort gefangenen 0-Gruppe) ist. In den übrigen Gebieten ist das Verhältnis (s. o.) ungefähr wie 1:3. Das Missverhältnis zwischen den Schollen der 0- und I-Gruppe im Skagerrack und nördlichen Kattegat wird durch Einwanderung bedeutender Mengen von einjährigen Schollen aus dem Skagerrack ins nördliche Kattegat, vornehmlich in einzelnen Jahren, erklärt. Eine solche Einwanderung ist schon von Johansen zur Erklärung von Unterschieden in der Zahl der Analflossenstrahlen von 0- und I-Gruppe im nördlichen Kattegat angenommen worden. Die Einwanderung soll so stark sein, dass im Mittel zwei Drittel der 0-Gruppe aus dem Skagerrack in das nördliche Kattegat auswandern. In gewissen Jahren ist auch in dem südlichen Kattegat und der Beltsee der Fang an I-Gruppe unverhältnismässig gross, verglichen mit dem an 0-Gruppe im vorhergehenden Jahre, sodass Verf. für diese Jahre eine Einwirkung der Auswanderung aus dem Skagerrack bis in die Beltsee annimmt. Wenn diese Anschauung des Verfassers durchaus zutrifft, so wird man, wie er richtig bemerkt, nicht, wie Blegvad es in seiner zweiten Arbeit getan hat, aus der Bestandszusammensetzung nach Altersgruppe Rückschlüsse machen dürfen auf die Quantität der Jahresbruten in diesen Gebieten. Nach Ansicht des Ref. würde aber auch Johansen durch gleichwertige Berücksichtigung der I-Gruppe sein Material unzuverlässiger gemacht haben. Ein gutes Beispiel ist hierfür die schon oben erwähnte Jahresgruppe 1921, die Blegvad reichlich fand, während sie in Johansen's Material etwas unter dem Durchschnitt blieb. Nach den Jungfischuntersuchungen war der Jahrgang in der Beltsee und im südlichen Kattegat als 0-Gruppe äusserst gering, die grösseren Zahlen treten erst in der I-Gruppe durch Einwanderung aus den nördlichen Gebieten auf.

Es scheint dem Referenten aber nicht ganz gesichert, ob aus diesen Untersuchungen so weitreichende Schlüsse zuverlässig gezogen werden können. Der Verf. nimmt für die Jahrgänge 1912 und 1921 solche Einwanderungen an und hat den Prozentsatz des I-Gruppenfanges von dem 0-Gruppenfang des vorhergehenden Jahre berechnet. Ergänzt man seine Angaben durch die Werte für Jahrgang 1911 und 1920, ergibt sich folgende Uebersicht:

Prozentsatz des Fanges an I-Gruppe vom 0-Gruppenfang des vorhergehenden Jahres.

Geburtsjahrgang	1911	1912	1920	1921
Skagerrack	6,1	7,0	51,9	5,4
Nördl. Kattegat	3,0	151,9	157,7	30,1
Südl. Kattegat	7,2	37,4	6,2	546,7
Beltsee	27,3	—	—	159,2

Man findet mehrfach ein inkongruentes Verhalten von 0- und I-Gruppe. Die Jahrgänge 1912 und 1921 werden vom Verfasser als Stütze seiner Anschauung aufgestellt. Es zeigt sich jedoch, dass in den anderen Fällen Inkongruenzen auftreten, die einer anderen Erklärung bedürfen. (Sehr geringer Prozentsatz I-Gruppe in allen Gebieten 1911.) Vielleicht können Untersuchungen über die Tiefenverbreitung der 0- und I-Gruppe in den verschiedenen Gebieten manche der noch herrschenden Zweifel lösen.

Sehr von Interesse sind natürlich die Befunde des Verfassers über die Grösse des 0-Gruppenfanges. Im Skagerrack war 1912, in den übrigen Gebieten 1911 beiweitem das beste Brutjahr. Ferner sind gute Jahre im Skagerrack 1905 und 1922, im nördlichen Kattegat 1921 und 1924, im südlichen Kattegat 1920, in der Beltsee 1913 und 1925. Schlechte Jahre dagegen waren im Skagerrack *1909*, 1920, 1924. Im nördlichen Kattegat 1909, *1913*, im Südkattegat 1914, 1921 und 1922, in der Beltsee *1912*, 1914, 1921, 1926. Ein Einfluss der Befischung auf die Menge der erzeugten Brut geht aus einem Vergleich der Vor- und Nachkriegsmittel nicht hervor.

Der Verfasser behandelt sodann die Jugendstadien von *Rhombus maximus*, *Rhombus laevis* und *Solea vulgaris*, die zusammen mit den Jungschollen gefangen worden sind. Er bemerkt jedoch, dass die Experimente auf den Fang der Schollen der 0-Gruppe abgestellt waren und für die anderen Arten, deren Vorzugsgebiete etwas anders liegen, nicht in gleichem Masse repräsentativ sind. Für den Steinbutt ist das Skagerrack das wichtigste Gebiet, für die beiden anderen Arten dagegen das nördliche Kattegat, das nach Ansicht des Autors mit seiner relativ hohen Temperatur für diese beiden Arten, die ein hauptsächlich südliches Verbreitungsgebiet haben, besonders günstig ist. Der Ausfall der Jahrgänge ist in jedem Gebiet für die drei Arten und für jede Art in den einzelnen Gebieten sehr verschieden. Für die Seezunge im Kattegat, wo nach E. Mohr die V-Gruppe in den Fängen am zahlreichsten ist, ist eine erträgliche Uebereinstimmung des Fanges mit der Menge der 0-Gruppe sechs Jahre früher zu beobachten.

Wir sehen in diesen vier Arbeiten viele sehr bedeutsame Erkenntnisse niedergelegt und zugleich zeigen sich Felder, wo weitere Arbeit zur Klärung noch ungelöster Fragen ansetzen muss.

Bruno Schulz und Alfred Wulff. Hydrographische und Planktologische Ergebnisse der Fahrt des Fischereischutzbootes "Zieten" in das Barentsmeer im August—September 1926. Ber. d. deutschen wiss. Komm. f. Meeresforschung, N. F. Bd. III, H. 3.

The Barents Sea has many analogies with the North Sea, not only in respect of natural conditions as a wide shallow-water area influenced by

admixture of waters of widely different origin, but also the fishery conditions are in a way similar, in so far as this sea supports a large trawl fishery by British as well as by German, Russian and even other trawlers. Hence a knowledge of the natural conditions of the Barents Sea is felt to be important by the three countries alluded to, and also by Norway on the coasts of which country the Barents Sea cod is exploited in the spawning stage. Russia has in a series of years both before the war and in the years 1921 up to the present, done a great deal to collect material towards an understanding of the oceanographic variations, especially by organizing quarterly surveys of what is regarded as a "critical" section, along the Kola meridian ($33^1/_2^\circ$ E.). Unfortunately it has not been possible to execute this very laudable programme in every instance, and the German cruises in these waters come therefore as a welcome complement to the Russian investigations and form in themselves important and thoroughgoing contributions to the general knowledge of this great and rich fishing area.

The work cited above contains two separate papers, on the hydrographical work by Schulz and on the plankton by Wulff.

Prof. Schulz gives an admirably clear statement of the salinity and temperature, illustrated by striking diagrams which show that the different branches of the "Gulf-Stream" water in Aug. 1926 occupied about the usual positions as revealed by the Russian investigations, except the third branch, which was very broad and extended about 30 miles farther north than usual, while the fourth (the Franz-Josef drift) was overlaid by a thick layer of relatively cold and fresh melting-water. In general the temperatures were found to be much higher than in 1906, but considerably lower than in 1921 and especially than in 1922, indicating very remarkable variations in the pulse of the Atlantic water. Prof. Schulz is struck by the wavy run of the isotherms and isohalines in the two sections (the meridians $33^1/_2^\circ$ and 38° E.) but is not much inclined to ascribe this feature to real wave movements along the meridians but rather to some effect of the channels in the bottom-relief. This question can not, however, according to Schulz' opinion be decided without a much more detailed study by a number of swiftly traversed sections, and till such a work can be carried out, no very great improvements can be gained in the diagrammatic picture of the currents drawn by Knipowitsch in 1905.

The plankton material from the cruise is reported on by Dr. Wulff, who following the old idea of using the plankton as an indication of the origin of the different watermasses, is able to show definitely that the bands of warmer and salter water are peopled by organisms from western areas and to arrive at several similar conclusions, thereby proving the oceanographic value of even such a restricted investigation as that made on the cruise of the Zieten, where only a small surface net was used. The plan was, however, to investigate the plankton in the depths by centrifuging water-samples. As far as the use of centrifuge went, all went well, but the vibrations set up by the motors proved fatal to the microscopical investigation, so that only very rough estimates as to the quantities present of the smallest plankton forms could be made. But so much was ascertained that these northern waters are peculiarly poor in nannoplankton both

as compared with the North Sea and with the rather high amounts of bigger phytoplankton forms gathered in the surface net. Dr. Wulff takes up the forms of the tintinnoid *Cyttarocylis denticulata* for closer scrutiny in relation to the different conditions obtaining in the various regions visited, and explains tentatively the great differences in size as responses to the greater or less viscosity of the water, the cold arctic waters being peopled predominantly by big forms.

Dr. Wulff ascribes the richness of the arctic zone in phytoplankton to the supposed great quantities of nutritient salts contained in the melting ice, but have determinations to prove this ever been made?

The speedy working up and publishing of the results of this cruise are very praiseworthy. O. Sund.

A. Wulff. Die chemischen und physikalischen Eigenschaften des Meerwassers. Reprint from: Tabulae Biologicae, ed. W. Junk, Vol. IV (1927).

Jeder Meeresforscher muss sich Dr. Wulff zu Dank verpflichtet fühlen wegen der grossen Mühe und Sorgfalt, die er sich gegeben hat, um diese grosse Fülle von zum Teil schwer auffindlichen Daten in einen kleinen Raum zusammenzubringen. Der sehr reichhaltige Inhalt des 80-seitigen Büchleins entspricht wirklich dem Titel — Ref. hat jedenfalls nichts erdenken können, das man darin zu finden vernünftigerweise verlangen könnte — und enthält ausserdem ein mehr als zwei dichtgedruckte Petitseiten einnehmendes Literaturverzeichnis mit in allem 162 Titeln. Eine Menge von Figuren und Beispielen erleichtern das Verständnis und eine Übersicht der Oceanographie des Atlantischen Oceans wird durch Wiedergabe von fünf Kartentafeln aus Schotts nunmehr in der 2. Aufl. erschienenen Geographie d. Atl. Ozeans gegeben. Wer jetzt noch nicht in die Ozeanographie eindringen kann, dem ist nicht zu helfen. O. S.

Robert Gill. The Influence of Plankton on the Phosphate Content of Stored Sea-Water. Journal of the Marine Biological Association, XIV, No. 4, pp. 1057—1065, 1927.

It is shown that the dissolved phosphate content of sea-water must be determined within a few days at most after sampling. If kept in the dark in bottles which yield no phosphate to distilled water, the phosphate content of the samples rises owing to the gradual disintegration of the organisms present. This increase in September off the Northumberland coast was found to be greater in the upper layers of the sea (c. 200 per cent. at 0 metres) than in the deeper water (12 per cent. at 70 metres) after standing in the dark for 10 days. Even in winter an increase of over 100 per cent. was observed after 65 days in the dark, the increase being 73 per cent. as deep as 70 metres. Plankton hauls made in conjunction with the first experiment agreed except at the surface and at 10 metres where the nets were too coarse to retain the phytoplankton. No hauls were made in conjunction with the second series though presumably plankton was

poor. The large increase in phosphate in these water samples is surprising. There is apparently as yet no suitable method for the preservation of water samples for phosphate analysis and results after storage must be interpreted with care. A. P. O.

F. P. Stowell. The Adsorption of Ions from Sea-Water by Sand. Journal of the Marine Biological Association, XIV, No. 4, pp. 955—966, 1927.

Starting from the observation that in a sea-water aquarium a slight concentration of the salts takes place in the sand of the filter beds, the author has examined the adsorption of these salts, first from sea-water and second from solutions of the individual constituents by a series of cleaned sands. The amount of adsorption from sea-water under standard conditions varies somewhat with the nature of the sand but the order of adsorption of the constituent ions is constant, viz. $Mg^{\cdot} > Na^{\cdot} > Ca^{\cdot}$ for cations and $Cl' > SO'_4$, HCO'_3 for anions. The position of $Ca^{\cdot}$ in the series is abnormal when compared with the series of Rona and Michaelis for adsorption of ions by charcoal. For all ions but $Ca^{\cdot}$ adsorption is therefore probably a physical phenomenon. The abnormal adsorption of $Ca^{\cdot}$ is to be explained by the fact that sand is not an inert adsorbing agent like charcoal and that continuous ionic interchange takes place between the $Mg^{\cdot}$ and to a lesser extent the $Na^{\cdot}$ in the sea-water and the calcium silicates in the sand. This is demonstrated by percolating solutions of sodium chloride and magnesium sulphate through the sand when calcium appears in the filtrate.

While the chief interest of the results is chemical the abnormal adsorption of $Ca^{\cdot}$ may possibly be of biological importance. A. P. O.

F. S. Russell. The Vertical Distribution of Plankton in the Sea. Biological Reviews, Vol. II, No. 3, June 1927. Cambridge.

The author gives in the present paper an account of our knowledge of the vertical distribution of plankton in the sea, reviewing the principal papers dealing with this question.

The literature about vertical distribution of plankton animals and plants in the sea is so extensive, that it has certainly been a very comprehensive work to collect and criticise all the more important observations made both in nature and in the laboratory in connection with this problem. The author gives the following plan for his work:

1) Information as to the various external factors that may or may not be of importance in controlling the vertical distribution of plankton organisms.
2) A general survey of our knowledge of the vertical distribution of plankton plants and animals in the sea, and the theories suggested by field observations.
3) The principal results obtained by experimental work, and the theoretical suggestions arising from them.

In the first section he discusses the various physical and chemical factors, which are supposed to have an influence upon the vertical distribution of plankton organisms and his conclusion is, that the most important external factors in this respect are light and temperature. The paper is primarily concerned with the behaviour of the zooplankton, but a short account of the vertical distribution of the phytoplankton is also inserted. Of considerable interest is a scheme given to illustrate the suggested classification of depth distribution of the different plankton communities according to various authors. As it has been shown by several investigators that the vertical distribution for any one species is not to be laid down within fixed limits but is liable to variation, the author has divided these variations under the following headings: 1) regional changes in vertical distribution, 2) seasonal changes, 3) daily changes, 4) ontogenetic changes, 5) changes due to spawning habits and 6) special variations due to hydrographical conditions. It is a very useful method to consider the different changes in vertical distribution in this way, stating briefly under the separate headings the various observations and explanations which have been put forward by the different authors. Concerning experimental observations on plankton animals the literature is fairly rich but the results of the various investigators are very often rather different, and the author emphasizes the point that it is necessary to know precisely the normal conditions under which the animals live in nature before studying the reactions in the laboratory. It seems most probable that light can be regarded as the most important controlling factor, but undoubtedly the question of vertical distribution in general is very complicated and we are very far from possessing a general theory explaining the whole problem. The author seems rightly to emphasize the point that far more observations in the field and in the laboratory are required, indicating how limited our knowledge really is about the behaviour and the distribution of plankton organisms in the sea. The importance of the present paper is very great, displaying as it does in a clear and useful manner our present knowledge from various points of view, and it will certainly serve as an incitement and point the way to lines of future research. P. Jespersen.

J. Travis Jenkins. The Herring and the Herring Fisheries. London, P. S. King & Son, Ltd. 1927.

The latest product of this fertile author deals with a subject that nowadays receives much attention. The bulk of the book is occupied by historical matter, only two chapters being devoted to the biology and the races of the herring. The present writer proposes to discuss these latter first.

The principal impression we get from reading these chapters on natural history is that they are somewhat fragmentary, as if the author has drawn his knowledge from occasional books, incidentally at his disposal. Hence it comes about that some subjects are treated in a cursory manner and others are unduly circumstantial. Why for instance dwell largely on the Arctic migration theory, now long since abandoned, and on the transportation of herring eggs to Southern countries? Why devote so much

space to the controversy as to whether the rings on the scales are true indications of age or whether they are merely an expression of the law of variability, to which latter view the author is inclined to give preference? To the general reader such discussions in a handbook must necessarily seem to confuse the whole matter. As to investigations of scales of sprat LUND (SUND?) is cited, but BJERKAN is altogether passed over in silence. Speaking of food of herring LISSNER is mentioned, but HARDY has apparently been forgotten. — By the way: the photograph of herring eggs opposite p. 18 is obviously enlarged, but this is not specially mentioned. The treatment of the herring races is in some points not very clear: it is of no value to give a tabular comparison between coastal and sea herring (p. 42) without stating that such measurements as are mentioned are antiquated, and that JOHANSEN's method of counting is by far the better. Bank herring of the North Sea are called "Scottish herring", a term somewhat misleading, and the Skagerrak herring ("almost [to] be regarded as the eastern variety of the Northern North Sea herring, as the Scottish herring may be regarded as the western variety") is stated to spawn on the Little Fisher Bank, whereas we now know that this happens only in occasional years, not regularly. Why LJUNGMANN (of 1874) is cited in regard to the herring fishery on the west coast of Sweden, and why PETTERSSON and EKMAN are not, is a mystery. The author contends: "this herring is now taken in large quantities by the German herring trawlers", though it is well known that the Germans of late have abandoned this winter fishery. The table on p. 29 in which the lengths of herring at the age of one, two years etc. are given is useless, in so far as it is not stated to which races the various samples, examined by a number of authors, apparently belonged.

The historical part of the book is really interesting, and the present writer has only to remark that the statement: "for the most part the Dutch boats fish for the so-called summer herring in the neighbourhood of Lowestoft" is on the same page (p. 76) contradicted by the words: "At the Scottish summer herring fishery a considerable number of Dutch herring boats are engaged." The fisheries of the middle ages, the Scania fishery, the rise and development of the present day industry — all this affords interesting reading and the author shows himself well versed in the literature. But passing on we get the vague impression that we have read already somewhere most of this history. Indeed many pages are wholly copied from the author's former book "The Sea Fisheries", which appeared in 1920. Here and there some passages are somewhat amplified or abbreviated. As an example of the first we may cite Chapter VI (The Fisheries Companies of the Stuarts) and Chapter IX (Trawling for herring). Such transcription also occurs in Chapter II (The Natural History of the herring), so that an obvious mistake in describing herring scales ("the other and posterior part is striated and has a number of concentric transparent semicircular zones, each bounded by a dark(!) ring") has passed over from "Sea Fisheries" into the present book (p. 25).

At the end of the last chapter the author mentions the International Council and the way it has worked during a quarter of a century. His adverse criticism is rather severe, we regret to say, so much so that it is stated: "Briefly, the International Council has, so far as the sea fisheries

are concerned, outlived its usefulness and should be replaced by some other organisation, or if left as at present, then it should be dissociated from bureaucratic control" (p. 152 – 153). The author's chief grievance seems to be that the scientific men charged with the research work are, by the fact alone that they are controlled and paid by State funds, under the necessity "of adjusting their views so that they will conform with official opinion" (p. 154). This is indeed a serious but really quite unjustified charge. Was there an "official" attitude in Great Britain towards herring trawling before the war? And what was the conclusion that English and Scottish investigators came to in their reports on the matter? Has any scientist employed by the State in any country after careful investigation, shrunk from expressing his honest view, if his opinion did not fall into line with preconceived ideas, provided that any such existed? Truly this whole accusation is unfounded and grievous to all those who have given whole-heartedly their time and their labour to the international fishery work. J. J. T.

H. Lissner. Die grosse Heringsfischerei in Deutschland. Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung. N. F. Bd. III. H. 4. 1927.

As a result of the enquiry made by Dr. Ehrenbaum and his fellow workers into the question of the German trawl fishing for herrings, it became evident that a careful study of the condition of German drift-net fishing for herrings was desirable. In particular it seemed necessary to examine whether the complaints made by the drift-net fishermen that their occupation was being injured by trawl fishing, and by excessive fishing for herrings in the North Sea were justified, or to what extent the decrease in the yearly catch of herrings was due to faulty methods or to the general economic conditions prevalent in the post-war period. It was thought that an examination of these conditions might lead to the discovery of means to help and improve the position of the German herring industry and to maintain in a healthy condition an important branch of German deep sea fisheries.

For the purpose of his enquiry, Dr. Lissner collected material partly through personal observation at sea on board the Fishery Protection Vessel "Zieten", and partly through a large number of records of voyages which were distributed through the fishing companies and filled up by the skippers of the fishing vessels. Of these latter he obtained about 250 records which covered about 300 separate voyages forming about 50 per cent. of the possible voyages in the period during which the records were taken.

The author has examined in detail the statistics of the fisheries in the western North Sea from the year 1894 to the year 1926 and he gives a comparative table covering the results of drift-net fishing and trawl fishing for Scotland, England, Holland, Germany and France, so far as these are available. It is noteworthy that the French statistics for recent years are very incomplete. He also examines the existing statistics of the herring fishing fleets in Scotland, England, Holland and Germany, and with regard

to this section of his enquiry he has collected together much very useful information. He also surveys the types of vessels and equipment used in the German fishing industry.

His enquiry covers an examination of the various fishing grounds used by the German drifters month by month, and this section of his work is accompanied by a series of useful charts. He points out that the fishermen themselves state that as a result of the introduction of trawling for herrings, and for other reasons, there has been a change in the German drift-net fishing grounds, but the author finds it difficult to prove that this is, in fact, the case. He notes, however, that there have been certain small changes in the fishing grounds, particularly between the Fladen Ground and the Dogger Bank. This latter change, however, he does not regard as being due to the development of trawling for herrings but as a result of experience showing that the grounds at present in use give better yields. Changes in the fishing grounds on the edge of the Dogger Bank are, however, to be definitely ascribed to the advent of trawling for herrings.

It is rare for vessels trawling for herrings to cause any damage to the drift nets.

As a result of his enquiry Dr. Lissner has reached the following conclusions. In comparison with the pre-war period the total catch of herrings has decreased in the western North Sea by approximately 40 per cent. The vessels engaged in herring fishing have also decreased to a corresponding extent as a result mainly of the constant diminution in the number of sailing drifters employed. The reasons are to be found in the changed economic conditions of the post-war period. An alteration has occurred in the biological position in that the normal size of herrings caught has become smaller. This is either due to the decrease in the amount of fishing which took place during the war or it may be the consequence of less food being available for the herrings in recent years. It is probable that a combination of factors has been in operation, but in the author's view, the development of trawl fishing for herrings cannot be held responsible for the change.

Dr. Lissner expresses the opinion that the German drift net fishing should be developed to the fullest possible extent in order to increase the proportion of herrings consumed in Germany, which are caught by vessels of German registration. Of the present annual consumption of salted herrings in Germany, only about 8 per cent. are cured from herrings caught on German vessels, while of the consumption of fresh herrings, some 25 per cent. are caught on German vessels. That there is room for the expansion of the industry is evident. Dr. Lissner's main suggestion for its development is a State loan to assist in the building of new vessels for drift net fishing. In his opinion, each company engaged in the fishing should possess from 20 to 25 vessels, and as there are at present in existence 10 companies possessing about 150 vessels, there are lacking between 50 and 100. He recommends that a loan of sufficient size to build at least 50 new vessels should be made by the State, and in his view the charges on such a loan could be readily borne by the industry. Efforts should be made to introduce the system of salting the herrings on board the vessels which are trawling for them, and he suggests that a subsidy per barrel equivalent to the import duty on herrings should be granted by the Government.

Such herrings should be branded with the mark "salted at sea". Dr. LISSNER further suggests that State aid should be granted for research voyages to find new fishing grounds, or that the German Herring Fishing-Boat-Owners' Society should undertake this research work at the expense of the companies affiliated to it. Finally he suggests that the herring fishing industry should be lightly treated by the Government as regards taxation and other burdens imposed by the State.

As regards the herring fishing practice he does not consider that the introduction of the Scottish net is essential but he recommends the decrease in the size of mesh in the drift nets used on the German vessels, and he also recommends the use of the English pattern leather buoy. He does not consider that the fishing grounds are always made best use of at the proper times, and he is of the opinion that an extension of the fishing season is both necessary and possible for the German vessels. He considers that an improvement in the organisation for the transmission of news between the herring fishing vessels and the ports would lead to better use being made of the fishing grounds and would lighten the work of the Fishery Protection Vessels. The wireless receiving apparatus as at present in use is regarded as being of little value, and wherever possible wireless telephony should be substituted. Where the cost of this is prohibitive on separate vessels, as is generally the case, the apparatus should be fitted on the leading vessel of a fleet.

Although Dr. LISSNER's paper brings to light little that is new, he has collected much valuable information and gives a clear and concise account of the present position and the needs of the German herring fishery, which will be of considerable use to workers in this field. B. W. P.

R. SPÄRCK. 1) On the Food Problem in relation to Marine Zoogeography. (Physiol. Papers ded. Prof. Aug. Krogh.) Copenhagen 1926.
2) Studies on the Biology of the Oyster (*Ostrea edulis*). II – IV. Rept. Dan. Biol. Stat. XXXIII. 1927.

1) Hitherto Zoogeography has been considered mainly from a systematic or phylogenetic standpoint. It was Dr. SPÄRCK's aim in writing this paper to stimulate greater interest in the food problem in relation to the Zoogeography of marine bottom animals.

From observations on oysters in aquaria and in tanks he concludes that the difficulties which occur at temperatures above about 20° C. are due to lack of sufficient food under these warm conditions, associated with which are paralysis of the adductor muscle, absence of the crystalline style, and a pale appearance of the digestive gland. Addition to the water of decaying *Zostera* and of glucose appeared to be effective in removing these symptoms.

These observations give rise to considerations of the food supply under natural conditions. SPÄRCK suggests that periodical summer mortalities on oyster beds, and the supplanting of *Ostrea edulis* by *O. angulata* on many of the beds in France, may be due to lack of food during warm periods, or where competition between species or with other genera is an important factor.

He also mentions the difficulty of rearing the larvae of *O. edulis* under conditions where larvae of Annelids and of other Lamellibranchs are able to thrive, suggesting that in natural waters the oyster larva comes off badly when competition for food is severe.

Other instances are given among Lamellibranchs where food supply appears to be the regulating factor in distribution, and where individuals of a species are larger in northern waters than those of the same species in a warm climate.

This short paper serves as a useful reminder of the scarcity of existing information about the natural supply and variations in quantity of food for such animals as the oyster, and the importance of this subject in relation to distribution. The increasing attention which is being given to the physiology of marine animals is likely to provide some basis for estimating food requirements at different temperatures, and advances in the study of Zoogeography may be anticipated in the direction suggested by the author.

2) This paper continues an earlier report, which was recently reviewed in this Journal (Vol. II, No. 1).

The first section deals with the feeding and growth of the pelagic larvae of *Ostrea edulis*. The economic value at the present time of a reliable method of procuring the settlement and growth of oyster spat needs no emphasis.

The author gives results of his experiments made on the rearing of oyster larvae in tanks from 1923—1926, first at Nykøbing, Mors, and later at the Danish Biological Station.

From the outset the main difficulty was recognised as that of feeding the larvae, rather than of inducing the oyster to spawn. Attempts made in tanks with warmed water, with daily renewal of water, and with filtered water proved fruitless. Certain nutrient solutions and emulsions and a culture of the diatom *Nitzschia minutissima* were tried in the laboratory with negative results.

Attention was then given to the value of small green organisms, which were present in open tanks where larvae contrasted favourably in vitality with those in covered tanks.

In July 1925 Dr. Spärck visited some of the Norwegian oyster pools where favourable conditions for production of spat are found, and noted the presence of a small unicellular green alga in considerably greater numbers there than in the Limfjord.

That summer, during a successful experiment by the English Fisheries Department at Conway, a similar alga (*Chlorella*), probably identical, was abundant. He obtained a sample and made cultures from it. The addition of this culture, which later contained other organisms, to the tanks in 1926, though associated with more satisfactory growth than occurred in preceding years, did not result in any settlement of spat. He is of opinion that the food conditions in spite of the measures taken presumably were not good enough, whether from the presence of too many other organisms or too great a growth of bacteria.

It has been noted, however, by the present reviewer during experiments at Conway that a settlement of spat may occur when the appearance of the water is clear and by no means suggestive of any great abundance of organisms. At the same time an excessive growth of a green alga such as

Phaeocystis on the bottom may raise the p_H considerably to a value above that which larvae can stand, viz: about 8.8. Any enrichment of tanks as suggested by Spärck has therefore to be carried out with considerable caution in order to avoid excessive alkalinity.

These experiments form a valuable series, but without any information regarding the p_H of the water, lack of food as the cause of failure must be accepted with reserve.

Section II contains observations on the conditions of the food supply of the oyster. The author mentions how, based on the examination of stomach contents, the view has been held till recently that finely divided particles of organic matter (detritus) must constitute the chief food of the oyster. This material was quantitatively predominant in the localities from which the stomach contents were examined. Spärck noted this predominance in the Limfjord, but his experiments in tanks, which at first appeared to confirm the older hypothesis later indicated that it was not detritus but green organisms especially flagellates on which the oysters fed. His observations in the Norwegian pools during July 1925 showed that stomachs there contained no detritus but almost exclusively green organisms, mainly *Prorocentrum micans*, with numerous smaller green planktonic algae and flagellates. Considering at the same time the recent work of Vonk and Yonge on digestion in the oyster, Spärck regards the evidence conclusive that oysters can feed solely on micro-organisms. Data on the extent to which in the Norwegian pools for instance, detritus or diatoms are available at other times of the year, would be of considerable interest.

The fattening of oysters in the French "claires" where diatoms seem to predominate is well-known.

The relative value of detritus, however, is at present obscure. It may, as Savage recently found, form at least 90 per cent. of stomach contents, but further work is required to demonstrate how the oyster uses this material as food.

Much work remains to be done on the feeding of the oyster, meanwhile Spärck's observations on the value of micro-organisms are a valuable contribution to the problem.

In his third section the author continues his earlier discussions on fluctuations in the oyster stock in the Limfjord, in which he sought to demonstrate a connection between periodicity of yield and changes in climatic conditions.

He now has available for comparison Hagmeier's survey of the West Slesvig oyster fishery. The fluctuations there show a marked coincidence with those in the Limfjord. In both localities there were periods of maximum yield round about 1870 and 1915, followed by marked decreases. This is regarded as confirmation of the theory that climate is the most weighty factor in determining good or bad periods, its influence extending over a large area. The importance of natural mortality, varying in extent according to locality is considerable, estimated at not less than 20 per cent. annually in the Limfjord, while fishing accounts for about 8 per cent. Cold is emphasised in connection with winter mortality under open water conditions, and food difficulties, predaceous animals, and overgrowth by competitors for food are presumed to account for summer mortality. H. P. S.

Current Bibliography.

Prepared by the Editor with the assistance of Miss Thursby-Pelham.

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in the North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given, but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

The classification of entries follows in a general way that adopted in Dr. ALLEN's Selected Bibliography published in Vol. I, Nos. 1 and 2 of the Journal, and since reprinted.

Subscribers and those on the distribution list will receive regularly upon application to the Administrative Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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Note.

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